Geographic variation and behavioral plasticity: Vigilance in desert bighorn sheep (Ovis canadensis nelsoni) populations

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GEOGRAPHIC VARIATION AND BEHAVIORAL PLASTICITY:
VIGILANCE IN DESERT BIGHORN SHEEP (OVIS CANADENSIS NELSONI) POPULATIONS

by

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A dissertation submitted in partial fulfillment
of the requirements for the

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ABSTRACT

Geographic Variation and Behavioral Plasticity: Vigilance in Desert Bighorn Sheep (*Ovis canadensis nelsoni*) Populations

by

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Antipredator behaviors such as vigilance are often costly because they must be traded off with other activities, such as feeding. To assess geographic patterns of vigilance behavior in bighorn sheep, I tested the large-scale hypothesis that vigilance in bighorn sheep would differ between populations as a result of spatial heterogeneity in predation regimes. Mean vigilance as well as the covariation of vigilance with environmental factors such as group size and distance from escape terrain were predicted to differ among regions with and without predators. Populations under high predation risk were three populations that had originally been translocated from a mountain range uninhabited by mountain lions to habitat with lions. Populations in habitat without resident mountain lions were three native populations in the Mojave Desert. Results indicated no difference in overall mean vigilance between populations of sheep in habitat with mountain lions verses those without lions. Instead, there were differences in vigilance between terrain types expressed at different group size. Although behavioral response to terrain type of large group size was consistent with adaptive vigilance
behavior, I rejected the hypothesis of large-scale adaptation and concluded that lack of population-level differences in overall vigilance was not consistent with predicted patterns of adaptive behavior.

To determine conditions that have prevented large-scale adulation, norms of reaction for vigilance of native populations were examined to determine whether vigilance in these populations reflects predicted patterns of adaptive behavioral plasticity due to the costs of maintaining vigilance in the absence of predators. Vigilance in translocated populations was examined to determine whether populations under relaxed predation pressure retained sufficient adaptive plasticity to adjust vigilance behavior in response to increased predation risk. Results indicated that the observed variability in adaptive responses among populations of native desert bighorn sheep with relaxed selection, combined with a nonadaptive response of sheep in one of the translocated populations, contributed to the overall pattern of non-adaptive variation in vigilance. Given that some populations exhibited adaptive norms of reaction for vigilance, it appears that there are a variety of processes and contingencies that combine to generate the observed variability in behavior of bighorn sheep.
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CHAPTER 1

INTRODUCTION

Behavioral ecology is based on the premise that natural selection maximizes gene survival, and that individuals (as temporary vehicles for genes) should behave in ways that maximize fitness (Krebs and Davies 1996). However, because conflicting selective pressures frequently play an important role in shaping the evolution of ecologically important traits, individuals cannot maximize all beneficial activities, but must instead balance conflicting demands (Shi 1987; Stearns 1992; Krebs and Davies 1996; Shi et al. 2003). For example, individual animals that forage under high predation risk trade off the risk of being killed by predators with the risk of starving.

Predation is a strong selective force in the evolution of antipredator behaviors (Magurran 1999). These behaviors are often costly because they must be traded off with other activities, such as feeding, resting, or looking for mates (Lima and Dill 1990). Of these, vigilance (scanning for predators) is one of the most intensively studied (Elgar 1989; Lima and Dill 1990). Vigilance is a phenotypically plastic trait that is both directly and indirectly linked to fitness (Lima and Dill 1990; Fitzgibbon 1989). Although animals may scan for other reasons (i.e. group cohesiveness) individuals that are less vigilant than their conspecifics are more susceptible to predation. Increased time spent in vigilance is time taken away from other fitness-related activities such as feeding (Fitzgibbon 1989;
Scheel 1993). In addition, a number of studies have shown that vigilance behavior for ungulates varies in response to local environmental factors that affect predation risk (Berger 1978; Lipetz and Beckoff 1982; Underwood 1982; Berger 1991; Bednekoff and Ritter 1994; Frid 1997; Burger and Gochfeld 1988; Burger et al. 2000).

The presence of predators is known to affect bighorn sheep by a sudden increase in vigilance (Stockwell 1991) and an increase in heart rate. Vigilance, as measured in this study, is not associated with the response to a predator’s presence, but with baseline or background levels of scanning for predators expressed by sheep in groups of different size and in different types of habitat. If vigilance behavior varies predictably with respect to group size or habitat, it can be considered to be phenotypically equivalent to a reversible plastic trait (Gomulkiewicz and Kirkpatrick 1992; Pigliucci 2002). Although the exact physiological mechanisms that control vigilance are unknown, they are likely to involve endocrine control, e.g., adrenaline production, (Kavaliers and Choleris 2001) and to be modified by external stimuli and experience. In this study, I assume the physiological set points of the control of vigilance and the degree that individual vigilance is influenced by external cues and learning, to result from a combination of genes and environment that can be modeled as a behavioral reaction norm (Gomulkiewicz and Kirkpatrick; Thompson 1999, Carroll and Corneli 1999, Pigliucci 2002).

Because of the conflicting selective pressures associated with antipredator behaviors, formerly adaptive antipredator behaviors can be lost when changes in predation regimes cause isolation of prey from predators (Coss 1999; Magurran 1999). The loss may be partial, occur over evolutionary time, or within an individual’s lifetime (Coss 1999;
Magurran 1999; Berger 1999; Hunter and Skinner 1998). Isolation of prey can occur when populations invade new habitats lacking a class of predators that were abundant in the environment of the source population (Coss 1999), or when historic predators, such as wolves and grizzly bears, have been extirpated from a region (Berger 1999). A change in predation regime may also occur when animals are translocated from habitat under one predation regime to habitat under another regime (Hunter and Skinner 1998).

Bighorn sheep (*Ovis canadensis*) are medium-sized ungulates of western North America that inhabit mountainous terrain from northern Alaska to Baja California and Sonora, Mexico (Geist 1971; Shackelton 1985). They rely on rocky, precipitous and usually non-forested terrain to detect and escape from predators (Geist 1971; Shackelton 1984). Natural predators include mountain lions, *Felis concolor*, coyotes, *Canis latrans*, bobcats, *Lynx rufus*, and wolves, *Canis lupus* (Logan and Sweanor 2001). Vigilance levels in bighorn sheep populations have been found to vary in response to location with respect to escape terrain (steep and/or rugged cliffs and slopes), presence of predators, visibility, and presence of neonates (Risenhoover and Bailey 1985; Berger 1991; Stockwell 1991). Vigilance is also affected by group size; with vigilance generally found to decrease as group size increases (Berger 1991; Warrick and Krausman 1987; Risenhoover and Bailey 1985). This relationship is attributed to benefits such as increased predator detection and a dilution effect (Hamilton 1971; Dehn 1990; Scheel 1993). These benefits are considered to be distinct but may interact with each other (Bednekoff and Lima 1998).

One of the most important variables affecting vigilance of bighorn sheep is relation to escape terrain. Berger (1991) found mortality from predation to be nearly three times
greater for ewes and lambs foraging at distances greater than 100 meters from escape terrain compared to those foraging closer to, or on escape terrain. Although vigilance is generally higher when the threat of predation is higher, the effect of predation risk factors on vigilance is interactive rather than additive, i.e., vigilance levels increase with decreasing group size but the distance from escape terrain determines the magnitude of the effect (Risenhoover and Bailey 1985; Frid 1997).

Efforts to restore extirpated sheep populations have relied greatly on translocation programs and, as a result, over 50% of all present day populations have originated from translocations (Bailey 1990; Jessup et al. 1995). A number of these animals have been transplanted from mountain ranges without predators to ranges occupied by mountain lions (Ashman et al. 1983). Mountain lions are capable of causing significant mortality in bighorn sheep populations and lion predation has had deleterious effects on the success of sheep restoration programs (Berger 1991; Wehausen 1996; Ross et al. 1997; Hayes et al. 2000; Logan and Sweanor 2001).

Given their importance as predators of bighorn sheep, I investigate how the presence of mountain lions influences the expression and evolution of vigilance behavior in bighorn sheep populations. One of the most effective ways to test adaptive hypotheses is to examine population responses across large geographic areas. Studies to determine the genetic basis of geographical variation are generally carried out by collecting organisms from environmentally different natural populations and raising their progeny in a uniform environment (Coss et al. 1993, Dunn and Robertson 1992; Endler 1986; Arnold 1981). Under these conditions, geographic differences can be attributed to genetic differences. This technique has been extended to study adaptive divergence of norms of reaction by
observing populations across a range of reciprocal environments (Carroll and Corneli
Collecting bighorn sheep from native populations and raising their progeny in reciprocal
environments is logistically, unfeasible. Instead, sheep populations that have been
transplanted from habitat without mountain lions into mountain ranges inhabited by lions
can be used to test hypotheses of large-scale adaptation or optimal behavioral allocation
by examining proximate causes of differences in mean reaction norms of vigilance levels
among populations. Although it is not possible to test whether vigilance norms of
reaction have evolved through natural selection, it is possible to determine if the
geographic patterns and covariation of vigilance with group size and habitat are
consistent with expectations of adaptive behavioral plasticity and population divergence.

I predicted that bighorn sheep populations in low-elevation mountain ranges
uninhabited by mountain lions would have low levels of vigilance due to the costs of
maintaining vigilance in the absence of predators. Mean vigilance as well as the
covariation of vigilance with environmental factors such as group size, and distance from
escape terrain, were predicted to differ among regions with and without predators based
on models of predator avoidance. To test these hypotheses I compared vigilance behavior
of three populations of native desert bighorn sheep inhabiting low-elevation mountain
ranges without resident mountain lions to vigilance behavior of three populations of
bighorn sheep translocated from a low-elevation Mojave Desert mountain range into
habitat with resident mountain lions.

In Chapter Two, I tested for predicted patterns of adaptive vigilance in desert bighorn
sheep populations inhabiting regions with and without large predators. I tested the large-
scale hypothesis of adaptive vigilance behavior in desert bighorn sheep populations transplanted from habitats without resident mountain lions to habitat with resident mountain lions. I predicted that bighorn sheep populations in low-elevation mountain ranges uninhabited by mountain lions would have lower levels of vigilance than populations in habitat with lions, due to the costs of maintaining vigilance in the absence of predators. I also examined vigilance response of bighorn sheep to covariates (group size and location in relation to escape terrain) that are predicted to affect vigilance. If there is a cost of being vigilant through loss of foraging efficiency, one would expect sheep populations in non-lion habitat, where risk of predation is less, to have lower mean vigilance levels than populations in mountain ranges inhabited by mountain lions. Sheep transplanted from low-elevation ranges into areas with mountain lions should show an increase in vigilance as populations adjust vigilance levels in response to the increase in predation risk. However, based on predictions from vigilance theory, sheep should also adjust vigilance in response to local environmental variables (group size, terrain, etc.). The magnitude of these behavioral responses will depend on the intensity of predation risk for each population. The effect of group size on vigilance will be more pronounced for populations in high predation risk mountain ranges, and the effect of location in relation to escape terrain will be greater for populations in high predation risk mountain ranges. Thus, in addition to differences in mean vigilance levels due solely to presence or absence of mountain lions, bighorn sheep populations could exhibit adaptive plasticity in vigilance that includes plastic change in the covariance of vigilance with ecological variables that yield an "optimal" response in all environments including habitats with or without mountain lions.
Behavioral phenotypes are the result of a complex combination of individual differences in genes affecting behavior and in an experiential environment that can be expressed as norms of reaction (Pigliucci 2001). Environmental variation can be both spatial and temporal (Gomulkiewicz and Kirkpatrick 1992). The norm of reaction for a genotype is the set of different behavioral phenotypes predictably expressed in response to each environment that an individual encounters. The phenotype represents the sum total of these strategies. Examples of the use of norms of reaction to study population-specific behavioral phenotypic plasticity can be found in Carroll and Corneli (1999) and Thompson (1999).

A lack of fit to predicted patterns of adaptive behavior of the three replicate populations in low-elevation mountain regions compared to the three replicate populations in high-elevation mountain regions could be due to high variance of vigilance among populations within low-elevation mountain ranges and persistence of vigilance despite relaxed selection, or it could be due to the lack of adaptation and lack of evolution of increased vigilance in the translocated populations occupying high-elevation mountain ranges. In the third and fourth chapters, I address population differences in vigilance in the presence and absence of mountain lions to determine conditions that may prevent large-scale adaptation.

In Chapter 3, I examine norms of reaction for vigilance of the three native bighorn sheep populations inhabiting low-elevation mountain ranges without resident mountain lions to determine whether vigilance behavior in these populations reflects predicted patterns of adaptive behavioral plasticity in vigilance due to the costs of maintaining vigilance in the absence of predators. Under relaxed predation, evolution of vigilance will
depend on the intensity of natural selection on foraging traits that are linked to vigilance through time trade-offs. The predictive hypothesis for the response of adaptive plasticity in vigilance due to the costs of maintaining vigilance in the absence of predators was that overall mean vigilance would be relatively low and the relationship between vigilance and its ecological covariates will have become weak or non-existent. Alternatively, if populations differ in the intensity of selection on vigilance as the result of historical differences in predation risk, or differences in the cost of vigilance, populations of bighorn sheep inhabiting areas without resident lions may exhibit a relatively low level of overall mean vigilance. However, such a population might maintain adaptive plasticity in vigilance that includes plastic change in the covariance of vigilance with ecological variables, or overall mean vigilance might remain high but the relationship between vigilance and its ecological covariates would become weak or non-existent. The null hypothesis is that there would be no adaptive pattern in vigilance behavior because there is no cost to vigilance in these populations. An alternative hypothesis is that there is random divergence among populations due to genetic drift, or a correlated response to selection of other unknown traits.

In Chapter 4, I examine vigilance behavior in sheep translocated from the River Mountains, Nevada, into habitat with resident mountain lions to determine whether populations under relaxed predation pressure have adequate adaptive plasticity to adjust vigilance behavior in response to increased predation risk. I assumed individual vigilance was a plastic trait and tested for population divergence in norms of reaction expressed across group size and terrain between source and translocated populations of bighorn sheep.
Translocated populations may exhibit adaptive plastic changes in vigilance that covary with ecological variables (terrain type and group size) to yield an "optimal" response for the new habitat that could be expressed immediately by most or all individuals, perhaps in response to habitat cues. Adaptive behavioral responses of vigilance behavior in translocated sheep populations could also increase over time due to cultural or maternal learning in response to predator encounters or due to evolution of vigilance plasticity such that the increase in vigilance would be positively correlated with duration of exposure to predators. If vigilance increases solely due to cultural transmission, it could change within a generation, whereas evolution of a heightened plastic response to predator encounters (heightened ability to learn or express vigilance) would occur over multiple generations as a response to natural selection.

Predictions for an adaptive plastic behavioral response to increased predation risk in translocated sheep populations were as follows: (1) there will be an immediate response to increased predation risk; mean vigilance and mean norms of reaction for vigilance expressed across environmental covariates of translocated populations will diverge from the source population and will be similar for all translocated populations, or; (2) translocated populations will show immediate partial divergence of mean vigilance and mean norms of reaction for vigilance expressed across environmental covariates followed by a pattern of increasing divergence in overall mean vigilance and mean reaction norms through time (i.e. with increasing age of translocation population). The null hypothesis was that there is no difference in natural selection of vigilance behavior and no divergence of mean vigilance between the source and translocated populations. An alternative hypothesis was that there is random divergence among populations due to
genetic drift, or a correlated response to selection of other unknown traits.

Results from this study can provide insight on how the presence or absence of large predators influences vigilance behavior in desert bighorn sheep populations.

Reintroduction is a major tool in the effort to conserve bighorn sheep populations.

Results from this study can also provide insight on the ability of translocated populations to adapt to new habitat conditions with higher predation risk. Although it is not possible to test whether vigilance norms of reaction have evolved through natural selection, results of this study can be used to determine if the geographic patterns and covariation of vigilance with group size and habitat are consistent with expectations of adaptive behavioral plasticity or optimal behavioral allocation.

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CHAPTER 2

VARIATION IN VIGILANCE BEHAVIOR OF DESERT BIGHORN SHEEP
AS A RESULT OF INCREASED PREDATION RISK

Abstract

In behavioral ecology, vigilance behavior is often assumed to be adaptive or
optimally allocated as a trade-off between the risk of predation and investment in other
activities such as foraging. As the first step in an assessment of geographic patterns of
vigilance behavior in bighorn sheep, I tested the large-scale hypothesis that vigilance in
bighorn sheep would differ between populations as a result of spatial heterogeneity in
predation regimes. My prediction was that, in comparison to high-elevation mountain
ranges inhabited by mountain lions, sheep populations in low-elevation mountain ranges,
without resident mountain lions, would have lower levels of vigilance due to the costs of
maintaining vigilance in the absence of predators. I also tested hypotheses about the
covariation of vigilance with environmental factors that are assumed to affect perceived
predation risk, such as group size and location with respect to escape terrain.

Sheep populations in habitats without resident mountain lions were native
populations. Populations under high predation risk, in habitats with mountain lions, were
populations that had originally been translocated from a mountain range uninhabited by
mountain lions. Time since translocation ranged from two to approximately twenty years.
mountain lions. Time since translocation ranged from two to approximately twenty years. Results indicated no difference in overall mean vigilance between populations of sheep in habitat with mountain lions versus those without lions. Instead, there were differences in vigilance between terrain types expressed at different group sizes. Results of statistical contrasts examining the main effect of escape terrain across all populations of sheep in both lion and non-lion habitat indicated that in habitat with mountain lions, there was a significant difference in vigilance levels for sheep foraging in large groups on or near escape terrain compared to sheep foraging away from escape terrain ($p < 0.045$). Based on these results I reject the hypothesis of large-scale adaptation and conclude that the lack of population-level differences in overall vigilance is not consistent with predicted patterns of adaptive behavior, although behavioral response to terrain type at large group size is consistent with adaptive vigilance behavior.

Introduction

Wild sheep throughout North America are subject to predation by a number of predators including, coyotes (*Canis latrans*), wolves (*Canis lupus*), mountain lions (*Felis concolor*), and eagles (*Aquila chrysaetos*), (Berger 1991; Wehausen 1996; Ross et al. 1997; Hayes et al. 2000; Logan and Sweanor 2001). Of these, only mountain lions are capable of preying upon all sex and age classes of bighorn sheep (Iriarte et al.1990; Murphy 1998) and of causing significant mortality in populations that occupy mountainous habitats (Berger 1991; Wehausen 1996; Ross et al. 1997; Hayes et al. 2000; Logan and Sweanor 2001). Given their importance as predators of bighorn sheep, I investigate how the presence of mountain lions influences the expression and evolution of
vigilance behavior in bighorn sheep populations. Many of the behavioral traits associated with predator detection and avoidance are considered to be adaptive and phenotypically plastic (Curio 1975; Lima and Dill 1990; Reichert and Hendrick 1990). Vigilance (scanning for predators) is considered a phenotypically plastic predator detection trait that is both directly and indirectly linked to fitness (Lima and Dill 1990; Fitzgibbon 1989). Individuals less vigilant than their conspecifics are more vulnerable to predation (Fitzgibbon 1989; Scheel 1993) but increasing the amount of time allocated to predator detection results in less time available for foraging (Stephens and Krebs 1986). In addition, a number of studies have shown that vigilance behavior for ungulates varies in response to local environmental factors that affect predation risk (Berger 1978; Lipetz and Beckoff 1982; Underwood 1982; Berger 1991; Bednekoff and Ritter 1994; Frid 1997; Burger and Gochfeld 1988; Burger et al. 2000).

These generalizations are relevant to bighorn sheep (Ovis canadensis), as it is known that foraging efficiency decreases as vigilance increases (Berger 1978; Risenhoover and Bailey 1985). Vigilance levels in bighorn sheep populations have been found to vary in response to location with respect to escape terrain (steep and/or rugged cliffs and slopes), presence of predators, visibility, and presence of neonates (Risenhoover and Bailey 1985; Berger 1991; Stockwell 1991). Vigilance is also affected by group size; with vigilance generally found to decrease as group size increases (Berger 1991; Warrick and Krausman 1987; Risenhoover and Bailey 1985). This relationship is attributed to benefits such as increased predator detection and a dilution effect (Hamilton 1971; Dehn 1990; Scheel 1993). These benefits are considered to be distinct but may interact with each other (Bednekoff and Lima 1998).
One of the most important variables affecting vigilance of bighorn sheep is proximity to escape terrain. Berger (1991) found mortality from predation to be nearly three times greater for ewes and lambs foraging at distances greater than 100 meters from escape terrain compared to those foraging closer to, or on escape terrain. Although vigilance is generally higher when the threat of predation is higher, the effect of predation risk factors on vigilance may be interactive rather than additive, i.e., vigilance levels increase with decreasing group size but the distance from escape terrain determines the magnitude of the effect (Risenhoover and Bailey 1985; Frid 1997).

The presence of predators is known to affect bighorn sheep by a sudden increase in vigilance (Stockwell 1991) and an increase in heart rate. Vigilance, as measured in this study, is not associated with the response to a predator's presence, but with baseline or background levels of scanning for predators expressed by sheep in groups of different size and in different types of habitat. If vigilance varies predictably with respect to group size or habitat, it can be considered to be equivalent to a reversible plastic trait (Gomulkiewicz and Kirkpatrick 1992; Pigliucci 2002). Although the exact physiological mechanisms that control vigilance are unknown, they are likely to involve endocrine control, e.g., adrenaline production, (Kavaliers and Choleris 2001) and to be modified by external stimuli and experience. In this study, I assume the physiological set points of control of vigilance and the degree that vigilance is influenced by external stimuli to result from a combination of genes and environment that can be modeled as a behavioral reaction norm (Gomulkeiwicz and Kirkpatrick 1992; Thompson 1999, Carroll and Corneli 1999, Pigliucci 2002).
Models describing optimal vigilance assume a trade-off between the benefits of investment in predator detection and investment in other behaviors, particularly foraging (Lima and Dill 1990). Optimality models assume that fixed or plastic phenotypes have evolved through natural selection, and most models assume there will be enough phenotypic variation and additive genetic variation in a population to result in an optimal solution (within constraints) that maximizes fitness (McNamara and Houston 1992; Pulliam et al. 1982; Packer and Abrams 1990; Parker and Smith 1990; Lima 1987; but see Pierce and Ollason 1987 and Mangel 1991). An optimal level of vigilance (generally quantified as the amount of time an animal spends looking with head up during a foraging bout) is predicted to occur when there is a “perfect” trade-off between food gain and predator avoidance (Pulliam et al. 1982; Stephens and Krebs 1986; Lima and Dill 1990).

Change through time in vigilance within a population could be due to both evolutionary and non-evolutionary processes. The evolution of optimal trait expression in response to natural selection is dependent on the amount of additive genetic variance for that trait (Falconer 1989). To date, estimates of heritability for vigilance in ungulate populations are unknown. Behavioral responses can also be the result of non-genetic cultural transmission within a population which could: (1) increase an individual’s fitness during its lifetime; (2) decrease individual’s fitness and thereby work in opposition to natural selection, or; (3) cause non-evolutionary change of traits that are selectively neutral (Papaj 1994). For the purposes of this study, the term adaptive will be used in a broad sense to describe a behavioral phenotype that matches expectations of optimal models and, thereby, may confer high fitness. Although it is not possible to test whether
vigilance norms of reaction have evolved through natural selection, it is possible to
determine if the geographic patterns and covariation of vigilance with group size and
habitat are consistent with expectations of adaptive behavioral plasticity and population
divergence.

**Predation of Bighorn Sheep**

A lack of exposure to predation over evolutionary time has been known to result in
reduced behavioral sensitivity of prey to predators (Giles and Huntingford 1984;
Magurran 1986; Sih 1986; Foster and Ploch 1990; Coss et al. 1993). Ungulates inhabiting
areas where large predators have been extirpated have been found to be naïve in
recognizing and avoiding reintroduced predators (Hunter and Skinner 1998; Berger et al.
2001). Prey from populations that had not encountered dangerous predators for as few as
50 to 130 years were highly vulnerable to initial encounters.

Many desert bighorn sheep (*Ovis canadensis nelsoni*) populations occupy low-
elevation mountain ranges in the Mojave Desert that are uninhabited by mountain lions
(Bradley and Baker 1967; Geist 1971; McQuivey 1978; Lesley and Douglas 1979). Historic predator pressure on these populations is unknown but mountain lions are
generally not present in low-elevation mountain ranges (< 2,000 m) that are uninhabited
by deer (Berger and Wehausen 1991). Bighorn sheep in these ranges have inhabited a
relatively stable environment since the end of the last glacial age; vegetation has
consisted of desert scrub communities for approximately 10,000 years (Spaulding 1990).

**Translocation of Bighorn Sheep in Nevada**

In Nevada, the historic distribution of desert bighorn sheep is based on documented
observations, petroglyph locations, and other archeological evidence (McQuivey 1978).
Compared to their historic distribution, the current range of desert mountain sheep has been reduced substantially since the 1800's (McQuivey 1978). Population declines have been attributed to diseases transmitted from domestic livestock, unregulated hunting, and habitat loss and fragmentation (McQuivey 1978; Gross et al. 2000; Krausman 2000). To reconstruct past population numbers, the Nevada Department of Wildlife has an active reintroduction program designed to repopulate mountain ranges considered to be historic sheep habitat. As of 1994, 971 bighorn sheep in Nevada have been transplanted into 24 formerly occupied mountain ranges (Cummings and Stevenson 1995).

The majority of desert-dwelling mountain sheep used as founder stock are taken from the River Mountains in the Lake Mead National Recreation Area, Nevada. The River Mountains are a typical low elevation Mojave Desert mountain range characterized by desert scrub and desert wash plant communities (Leslie and Douglas 1979). Sheep from these mountains have been reintroduced throughout the state of Nevada and have also been used as founder stock for transplant operations in Colorado, Utah, and Texas. Habitat at relocation sites may or may not be similar to that of the River Mountains. A number of these animals have been transplanted into mountain ranges with substantial areas of pinyon-juniper woodland and ponderosa pine forest; these ranges are also occupied by mountain lions (Ashman et al. 1983). Mountain lion predation has had deleterious effects on the success of sheep restoration programs. When 22 bighorn sheep from the River Mountains in southern Nevada were released into Zion National Park, Utah, mountain lions killed 20% within the first 6 months (McCutchen 1979) and in the Wassuk and Snake Ranges of northern Nevada, bighorn sheep introductions failed because of lion predation (Berger and Wehausen 1991). In the River Mountains,
mountain lions have been sighted rarely, but these animals were migrants, not residents (Leslie and Douglas 1979).

Objectives and Predictions

In this chapter, I measure variation of vigilance among desert bighorn sheep populations to determine if geographic patterns match the predictions of models of optimal vigilance. Mean vigilance, as well as the covariation of vigilance with environmental factors such as group size, and distance from escape terrain, is predicted to differ among regions with and without predators based on models of predator avoidance. If there is a cost of being vigilant through loss of foraging efficiency, it can be predicted that sheep populations in non-lion habitat, where risk of predation is less, will have lower mean vigilance levels than populations in mountain ranges inhabited by mountain lions.

Sheep transplanted from low-elevation ranges into areas with mountain lions should show an increase in vigilance as populations adjust vigilance levels in response to the increase in predation risk. However, based on predictions from vigilance theory, sheep should also adjust vigilance within populations in response to group size and escape terrain, although the magnitude of these behavioral responses will depend on the intensity of predation risk for each population. The predictions for within-population adjustments are: 1) vigilance will decrease with increasing group size, and 2) for a given group size, vigilance will increase with increased distance from escape terrain (i.e. steep, rocky slopes). Thus, in addition to differences in mean vigilance levels of populations due solely to presence or absence of mountain lions, bighorn sheep populations could exhibit plasticity in vigilance that include plastic change in the covariance of vigilance with
ecological variables that yields an "optimal" response in all environments including habitats with or without mountain lions.

To test these predictions I compared vigilance behavior of three populations of native desert bighorn sheep inhabiting low-elevation mountain ranges without resident mountain lions to vigilance behavior of three populations of bighorn sheep translocated from a low-elevation Mojave Desert mountain range into habitat with resident mountain lions. In subsequent chapters, I examine patterns within populations to determine potential causes of variation in vigilance among populations.

Methods and Analysis

Study Sites

Vigilance behavior was sampled from six populations of desert bighorn sheep (Figure 1). Three populations from the River and Muddy Mountains, Nevada and the Eagle Mountains, California, were located in low-elevation mountain ranges in the Mojave Desert. These areas were uninhabited by resident mountain lions. Populations in the Delamar and Pancake Ranges in Nevada, and in Zion National Park, Utah, were originally translocated from the River Mountains. Translocation sites are inhabited by resident mountain lions (Table 1). Smaller predators, such as coyotes and golden eagles, were present in all mountain ranges. Originally, the study design included native sheep populations inhabiting mountain ranges with resident lions, but populations in these ranges (San Gabriel Mountains, and Granite Mountains, California, and the Clark/Kingston Mountains, Nevada/California), suffered severe population declines as
Figure 1  Map showing locations of native and translocated bighorn sheep populations included in this study. Ecoregions from Omernik (1987).
result of lion predation and habitat changes (Wehausen 1996), which made data collection from these populations unfeasible.

**Behavior**

Behavioral data were collected from bighorn sheep in the River Mountains during 1987 and 1988 and data from the remaining five mountain ranges were from 1995 through 2000. Vigilance levels were quantified as the proportion of time during a foraging bout that an animal stopped feeding to raise its head above the shoulders and look around at the surrounding terrain. Vigilance behavior of bighorn sheep was observed and recorded using a combination of focal animal and scan sampling techniques (Altmann 1974). To eliminate variance associated with differences between ewe and ram behavior, data were collected from ewes only. Ewes were also selected because they are subject a higher proportion of deaths due to predation than are rams (Berger 1991). Records were made of location, distance from the base of the nearest mountainside or rugged cliff (termed “escape terrain”), vegetation type within 2 meters, group size, and composition. Visibility, or the amount of visual obstruction due to vegetation cover, was not included in the analysis because vegetation measurably affected visibility in only two areas, Zion National Park and the Pancake Range. In the River Mountains visibility was only affected when ewes were feeding on acacia trees.

Once a group of sheep were located and > 60% of the animals were feeding, a focal animal was randomly selected and observed continuously for 5 minutes (300 sec). Sheep were observed with a Celestron C-5 telescope (90 power) and could be easily seen from over one half mile. Data were only collected on animals that were unaware of my presence and I made an effort to collect data as far from the animals as possible.
Table 1. Desert bighorn sheep populations used in the study. Transplant populations were reintroduced into historic sheep habitat which was uninhabited by bighorn sheep at the time of the reintroductions. Bighorn sheep translocated into the Pancake Range were not monitored closely after release. Although the Nevada Division of Wildlife has received a number of reports of sheep killed by lions in the Pancake Range, the exact number of confirmed deaths is unknown.

<table>
<thead>
<tr>
<th>Mountain Range (Population)</th>
<th>Geographic Location</th>
<th>Transplant History Number of Sheep Released. (Year of Release)</th>
<th>Confirmed Deaths Due to Mountain Lion Predation Within 2 Years of Release</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Habitat Without Resident Mountain Lions</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>River Mountains</td>
<td>Mojave Desert</td>
<td>Native Population (Transplant Source)</td>
<td>N/A</td>
</tr>
<tr>
<td>Eagle Mountains</td>
<td>Mojave Desert</td>
<td>Native population</td>
<td>N/A</td>
</tr>
<tr>
<td>Muddy Mountains</td>
<td>Mojave Desert</td>
<td>Native population</td>
<td>N/A</td>
</tr>
<tr>
<td><strong>Habitat With Resident Mountain Lions</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Delamar Range</td>
<td>Great Basin Desert</td>
<td>15 Ewes, 4 Rams (1997)</td>
<td>1 minimum*</td>
</tr>
<tr>
<td>Zion National Park</td>
<td>Colorado Plateau</td>
<td>30 animals released (1977 and 1979)</td>
<td>5</td>
</tr>
</tbody>
</table>

*A lion killed one of 5 ewes fitted with a radio telemetry collar.

**Mountain lion tracks were observed in areas occupied by sheep during this study.
Observations were only made on sheep that did not show signs that they had observed me. If animals were observed looking directly towards me in a non-random fashion, I did not collect behavioral data because I was interested in the overall, or general vigilance maintained in each population and not the response of ewes to a human observer. In addition, it is also possible that, depending on their degree of acclimation to humans, a population of sheep may react less alarmingly to a human observer than to a potential predator.

All behavioral activities were recorded continuously into a tape recorder. A focal animal was defined as vigilant when it lifted its head to shoulder height and surveyed its surroundings. Following the focal animal sample, another ewe was randomly chosen, excluding the previous animal until all members of the group had been observed. No attempt was made to discriminate between ‘active’ versus ‘weak’ vigilance (Alados 1985), determine whether vigilance was directed at specific objects (Lagory 1986), or whether sheep were engaged in decision-making concerning moving to other foraging patches (e.g. in buffalo Syncerus caffer; Prins 1996). Instead, I assumed that ewes were using the head-up posture to gather information on all possible factors. Behavioral data were transcribed using a stopwatch to measure scan durations to the nearest second and enable calculation of the proportion of time spent vigilant.

**Statistical Analysis**

Tests of the large-scale hypotheses of adaptive variation in vigilance (i.e., percentage of potential foraging time spent being “vigilant”) of bighorn sheep in response to differences in predator risk were performed using analysis of covariance and followed the technique described in Littell et al. (2001). Presence or absence of resident mountain
lions and relation to escape terrain, (on escape terrain or ≤100 m verses >100 m from escape terrain) were main effects, and group size was treated as a covariate. Prior to the analysis, vigilance was arcsine transformed to meet assumptions of normality and homogeneity of variance (Zar 1999). The assumption of homogeneous variance was evaluated with a plot of the residuals versus the estimated treatment means. Residuals were examined to verify normality and used to provide visual evaluations of the analysis of variance assumptions for homogeneous variances and normal distribution of experimental errors.

Analysis of covariance is a method of comparing a series of regression models to analyze data from a designed experiment where one or more continuous variables are measured for each experimental unit (Littell et al. 2001). The basic series of models consists of a different regression model for each treatment or treatment combination in the treatment structure. The approach outlined by Littell et al. (2001, pg 171) uses the mixed procedure in SAS (PROC MIXED, SAS Institute 2000) to first determine the form of the covariate in the model and then make comparisons between the regression models. The form of the covariate is determined by testing the hypothesis that the slopes are equal to zero. If the slopes are equal to zero, the covariate should not be included in the model. If the slopes-equal-to-zero hypothesis is rejected, the next step is to test the hypothesis that the slopes are equal. If the data do not fit a common slopes model an unequal slopes model was then fitted to the data (see below).

Estimates of both the slopes and intercepts are needed to test the slopes-equal-to-zero hypothesis. To provide estimates of the intercepts and slopes, the model fitted to the data by PROC MIXED must have a nonsingular design matrix. To accomplish this, the no
intercept option was included and the covariate was excluded from the model (Littell et al. 2001). The model statement for the slopes-equal-to-zero hypothesis included the main effects and the covariate-by-main-effect interactions. The Type III F-statistic corresponding to the covariate-by-main-effects interactions was used to test whether slopes of the covariate were significantly different from zero. A significant interaction indicated whether the covariate was needed in the model.

**Common and Unequal Slopes Models**

If the slopes-equal-to-zero hypothesis was rejected, the next step was to determine whether a model with a common slope could be used to describe the data. In models with common slopes (equal slopes hypothesis), regression models form a series of parallel lines and can be compared by estimating the distance between them (Littell et al. 2001). Differences among adjusted means of regression models with a common slope only involve the intercepts, and thus are independent of the value of the covariate used to compute the adjusted means (Littell et al. 2001). The covariate term is excluded, which enables the covariate part of the model to be nonsingular, thus providing estimates of the slopes. The model statement includes the main effects, covariate and main effect by covariate interaction. The Type III F-statistics corresponding to the interaction term were used to test whether the slopes were equal. A significant interaction indicated slopes of the covariate were unequal.

If the common slopes hypothesis was rejected, an unequal slopes model (termed the covariate-by-treatment interaction model) was used to fit the data (Littell et al. 2001). For regression models with unequal slopes, the comparison of each main effect of unequal slopes models depends on the value of the covariate and differences among adjusted
means involve both the intercept and slope. A multiple comparison procedure was performed on the slopes by comparing interaction-adjusted means rather than the main effect adjusted means. The models were compared at a minimum of three values (low, medium and high) of the covariate. The Satterwaite approximation, which depends on the values of the covariate where the models are being compared, was used to provide degrees of freedom for the denominators of each test statistic and for each estimated standard error (Littell et al. 2001).

Results

Total mean for vigilance of bighorn sheep was 15.1% ±0.5% (S.E.), (n = 534). The frequency of the distribution of time bighorn ewes were vigilant during foraging is in Figure 2. Mean vigilance of all populations in habitat with lions (n = 242) was 14.5% +1.15% and ranged from 0.0 to 61.3%. Mean vigilance of populations without mountain lions (n = 292) was 11.7 ± 0.9, (range 0 to 58.4%). Mean vigilance of bighorn sheep foraging on or near escape terrain (≤ 100 m) was 10.3 ± 1.1 (range of 0 to 35.4%), and for bighorn sheep foraging greater than 100 meters away from escape terrain mean vigilance was 11.7% + 0.9% (S.E.) and ranged from 0.0 to 49.8%.

Overall, group size was larger when ewes foraged under conditions of greatest perceived predation risk, i.e., in areas with mountain lions and away from escape terrain. Total mean adult group size was 9.6 and ranged from 1 to 40 adult sheep. Mean group size of adult bighorn sheep in habitat with resident mountain lions was 11 (n = 50 groups; range = 3 to 40 adults) and was higher (t = -2.9, P = 0.003) than mean group size of sheep in habitat without resident lions (mean group size = 8 adult sheep, n = 119; range = 1-30.
Figure 2. Frequency distributions of the percent time desert bighorn ewes were vigilant during a foraging bout in habitat with, and without large predators. Bighorn ewes were from three populations in areas inhabited by resident mountain lions and three populations in areas uninhabited by resident mountain lions.
Mean adult group size of sheep foraging on or near escape terrain (mean = 6; range 2 – 13; n = 44) was significantly smaller ($t = 2.82, P = 0.005$) than mean adult group size of sheep foraging away from escape terrain (mean = 10; range 1 to 40; n = 100). Mean group size for sheep foraging on escape terrain (mean = 6; range 2 – 13; n = 25) in habitat without resident mountain lions, was significantly smaller ($t = 2.033; P = 0.0045$) from mean group size away from escape terrain (mean = 9; range 1-30; n = 74). In habitat with resident mountain lions, mean group size of sheep foraging away from escape terrain (mean = 13; range = 3 – 40; n = 26) was higher ($t = 2.68; P = 0.0103$) than mean group size of sheep foraging on escape terrain (n = 19; mean = 7; range 2-3).

Results of the slopes-equal-to-zero model show a significant interaction between group size, presence of mountain lions, and escape terrain ($F_{4,523} =2.89; P =0.022$) indicating that the slopes and intercepts are not all equal to zero and that group size should be included as a covariate in the model. The equal slopes hypothesis was also rejected due to a significant group size by terrain interaction ($F_{4,524} =3.87; P =0.05$), suggesting that the relationship between group size and vigilance was not the same across all terrains (Figure 3). Accordingly, a multiple comparison procedure on the slopes was performed using the unequal slopes model. Mean vigilance was compared at low, medium, and high group sizes of 4, 9, and 14 (Figure 4). These values were chosen to include a range of group sizes that would fit all populations in the analysis.

To test the hypothesis of variation in vigilance behavior as a result of increased predation risk, multiple contrasts were used to compare overall mean vigilance in populations of desert bighorn sheep inhabiting areas with and without resident mountain lions at each of the selected group size values. Multiple comparisons were used to compare vigilance in
relation to escape terrain within each predation type at group sizes of 4, 9, and 14 and obtain adjusted means for combinations of lion/no lion and on or away from escape terrain at the three group size values.

Results of the comparisons showed no significant differences in mean vigilance levels between ewes in populations with and without resident mountain lions for any of the three group size values (Table 2). Results of the contrasts examining the main effect of escape terrain across all populations of sheep in both lion and non-lion habitat indicated a significant difference in vigilance levels at group size 14 for ewes foraging on or less than 100 m from escape terrain compared to sheep foraging greater than 100 m from escape terrain ($p<0.045$) (Table 2). Bighorn ewes foraging in large groups on or near escape terrain were less vigilant than ewes foraging away from escape terrain (Figure 4).

The difference was only significant for populations inhabiting areas occupied by resident mountain lions, indicating that vigilance response to escape terrain is consistent with adaptive predictions. Pairwise comparisons of terrain type (escape terrain verses non-escape terrain) across all populations in lion and non-lion habitat at the three group size values indicated an interactive effect of terrain and group size at the group size value of 14 ($P<0.056$). In habitat with resident mountain lions, large groups of bighorn ewes foraging greater than 100 meters from escape terrain were more vigilant than large groups foraging on or less than 100 meters from escape terrain. Vigilance of ewes in small and medium sized groups did not differ in relation to distance from escape terrain or the presence or absence of mountain lions.
Figure 3. Effects of group size and relation to escape terrain on vigilance of ewes foraging in habitat with and without mountain lions. Relation to escape terrain was categorized as on or less than 100 meters from escape terrain (on or near escape terrain) and greater than 100 meters from escape terrain (away from escape terrain).
Figure 4. Mean norms of reaction for adjusted mean vigilance (percent of total time spent vigilant during a foraging bout) of ewes foraging in non-escape terrain (greater than 100 meters from cliffs and steep, rocky slopes) and in escape terrain (less than 100 meters from cliffs and steep rocky slopes), across all lion presence conditions. The results in the figure are adjusted means computed at three values from each of the different regression models. Error bars represent standard errors.
Table 2 Results of the comparisons of main effects for mean vigilance (percent of total time spent vigilant) between desert bighorn ewes in populations with and without resident mountain lions. Adjusted mean vigilance was compared at three group size values from each of the different regression models. Degrees of freedom were determined using the Satterwaite approximation. Terrain types are greater than 100 meters from escape terrain and on or less than 100 meters from escape terrain (cliffs, or steep, rocky slopes).

<table>
<thead>
<tr>
<th>Contrasts for Main Effects</th>
<th>Covariate value (Group size)</th>
<th>Adjusted Mean (± SE) Lions</th>
<th>Adjusted Mean (± SE) No Lions</th>
<th>Degrees freedom</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lion vs. No Lion (across all terrain types)</td>
<td>4</td>
<td>22.1 (±3.3)</td>
<td>22.6 (±2.0)</td>
<td>4.29</td>
<td>0.584</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>20.7 (±3.6)</td>
<td>21.3 (±2.4)</td>
<td>6.12</td>
<td>0.319</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>19.4 (±3.9)</td>
<td>19.9 (±2.4)</td>
<td>9.08</td>
<td>0.584</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Escape vs. Non-Escape Terrain</td>
<td>4</td>
<td>22.6 (±1.3)</td>
<td>22.2 (±2.5)</td>
<td>491</td>
<td>0.765</td>
</tr>
<tr>
<td>(across all lion conditions)</td>
<td>9</td>
<td>20.3 (±1.2)</td>
<td>21.7 (±2.4)</td>
<td>443</td>
<td>0.195</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>18.1 (±1.5)</td>
<td>21.2 (±2.4)</td>
<td>485</td>
<td>0.045</td>
</tr>
</tbody>
</table>
Table 3. Results of the pairwise comparisons for mean vigilance (percent time spent being vigilant during a foraging bout) between ewes in populations with and without resident mountain lions. Adjusted mean vigilance was compared at three group size values from each of the different regression models. Degrees of freedom were determined using the Satterwaite approximation. Terrain types are categorized as escape terrain (on, or less than 100 meters from escape terrain) and non-escape terrain (greater than 100 meters from escape terrain). Escape terrain was defined as cliffs or steep, rocky slopes.

<table>
<thead>
<tr>
<th>Covariate value (Group size)</th>
<th>Adjusted Mean (± SE) Escape Terrain</th>
<th>Adjusted Mean (± SE) Non-escape Terrain</th>
<th>Degrees of freedom</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lions Present 4</td>
<td>21.9 (±2.5)</td>
<td>22.3 (±2.5)</td>
<td>434</td>
<td>0.861</td>
</tr>
<tr>
<td>Lions Present 9</td>
<td>19.7 (±2.4)</td>
<td>21.8 (±2.5)</td>
<td>383</td>
<td>0.860</td>
</tr>
<tr>
<td>Lions Present 14</td>
<td>17.5 (±2.6)</td>
<td>21.2 (±2.4)</td>
<td>409</td>
<td>0.056</td>
</tr>
<tr>
<td>No Resident Lions 4</td>
<td>23.2 (±2.3)</td>
<td>22.1 (±2.4)</td>
<td>495</td>
<td>0.463</td>
</tr>
<tr>
<td>No Resident Lions 9</td>
<td>21.0 (±2.3)</td>
<td>21.6 (±2.4)</td>
<td>485</td>
<td>0.687</td>
</tr>
<tr>
<td>No Resident Lions 14</td>
<td>18.6 (±2.5)</td>
<td>21.1 (±2.4)</td>
<td>509</td>
<td>0.200</td>
</tr>
</tbody>
</table>
Discussion

I tested the hypothesis of large-scale differences in mean vigilance behavior of bighorn sheep populations as a result of spatial heterogeneity in predation risk. Differences between populations were predicted to occur due to a combination of behavioral adjustments to optimize vigilance in both lion and non-lion habitat. The predictive hypothesis was that sheep populations in low-elevation mountain ranges that were uninhabited by resident mountain lions would have lower levels of vigilance due to the reduced costs of maintaining vigilance in the absence of predators. Ewes in populations translocated into habitats with mountain lions were predicted to increase overall mean vigilance as response to increased predation risk. Mean vigilance between habitats with and without lions was predicted to differ under the following assumptions: 1) there would be natural selection for vigilance due to increased predation risk from mountain lions; and 2) there was a cost to vigilance through loss of foraging efficiency. I also tested hypotheses about the plastic adjustment of vigilance in response to group size and relation to escape terrain. I assumed individual vigilance is a plastic trait and tested for population differences in vigilance response expressed across group size or types of terrain.

Results of the covariance analysis showed no differences in mean vigilance between populations in habitat with low versus high predation risk. These results were inconsistent with the predictions of optimal behavior or adaptive hypotheses. Ewes from populations of sheep transplanted into habitat with resident mountain lions were not more vigilant than ewes from populations without mountain lions. However, there was evidence of a plastic adjustment of vigilance in response to local environmental variables for sheep populations under predation risk from mountain lions. This behavioral adjustment

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resulted in differences between terrain types in vigilance response expressed at different group sizes. In areas with resident mountain lions, ewes foraging in large groups away from escape terrain were more vigilant than those under similar circumstances in mountain ranges without lions.

**Total Mean Vigilance**

Although results from previous studies suggest that response to relaxed selection from major predators is somewhat unpredictable (Coss 1999), variation in vigilance due to relaxed predation has been documented for ungulate populations. Caribou (*Rangifer rangifer*) in Alaska that are sympatric with wolves (*Canis lupus*) have much higher vigilance than conspecifics from western Greenland, where wolves have been absent for 4,000 years (Boving and Post 1997). Antipredator responses of moose subject to predation by wolves and bears in Alaska are greater (characterized by higher vigilance and defensive responses to auditory and olfactory cues of bears and wolves) than that of moose populations in Yellowstone National Park, where predators had been extirpated for 40-75 years (Berger et al. 2001). In this study, with 534 behavioral observations in six populations, the lack of significant differences in total mean vigilance of the three replicate populations in low-elevation mountain regions compared to the three replicate populations in high-elevation mountain regions could be due to (1) high variance of vigilance among populations within low-elevation desert mountain ranges, (2) persistence of vigilance despite relaxed predation, or (3) to the lack of increased vigilance in the transplanted populations occupying high-elevation mountain ranges.

Although mountain lions are not considered permanent residents in mountain ranges uninhabited by deer, there are rare sightings of lions in low-elevation ranges in
southern Nevada (based on reports to the Nevada Division of Wildlife, Pat Cummings, pers. comm. 2003) and it is possible that ewes in these populations experience a minimal amount of predation from occasional lions to offset the cost to vigilance in loss of foraging time. Variance in predation intensity among these populations may explain behavioral responses that do not match predictions for large-scale differences in vigilance. Underwood (1982) suggested that even when the likelihood of predation is low, vigilance in ungulates nonetheless appears to be affected by the possibility of predation. In his study of vigilance in African ungulates, where predation risk was low, animals still adjusted vigilance and its covariance with environmental factors to perceived predation risk. Kavaliers and Choleris (2001) suggest that animals may adaptively overestimate the risk of predation to avoid the relatively high cost of underestimation. Predation rates on sheep populations subject to lion predation were unknown, but predation on ewes by mountain lions was documented in two of the three populations (Zion N.P. and the Delamar Range). In the Pancake Range, mountain lion tracks were observed in sheep habitat during this study and evidence of lion kills have been recorded by Nevada Division of Wildlife personnel throughout the past ten years (Pat Cummins pers. comm. 2001).

**Vigilance Response to Group Size and Terrain Type**

Bighorn sheep ewes from populations under high predation risk display plastic adjustments of vigilance in response to group size and terrain variables that are generally consistent with optimal or adaptive predictions in habitat with predation risk from mountain lions. Vigilance decreased under conditions of lowest predation risk, when ewes in large groups foraged on or near escape terrain. Adaptive adjustments in vigilance
for small and medium groups did not occur. The lack of adaptive adjustments for medium and small group sizes could indicate that populations are currently at adaptive optima due to high intensity of natural selection for vigilance, or that there has not been enough time for these populations to reach adaptive optima. If populations are not at adaptive optima, further adjustments might occur over time due to evolutionary change or cultural or maternal learning in response to predator encounters. If vigilance increases solely due to learning (cultural transmission), these adjustments could occur within generations, whereas evolution of a heightened plastic response to predator encounters (heightened ability to learn) would occur over generations.

Ewes in habitat without resident mountain lions did not adjust vigilance to changes in group size or in relation to escape terrain, consistent with predictions of selection to decrease vigilance adjustments. However, this is unlikely given that overall mean vigilance of bighorn sheep was not lower in non-lion compared to lion mountain ranges and the flat slope of the vigilance response to group size in non-lion habitat could be the result of processes other than direct selection.

**Group Size**

Group size is a function of predator pressure and spatial placement of resources (Hamilton 1971). Group sizes of ewes in this study were largest in habitat with mountain lions and when sheep foraged away from escape terrain, both conditions of high predation risk. This pattern occurred regardless of vigilance levels. Because individuals in larger groups are thought to be less susceptible to predation, ewes foraging in habitat with resident mountain lions or away from escape terrain may lower individual predation risk by forming larger groups without adjusting vigilance, which may be of particular
importance if vigilance levels are already at maximum. Of course, habitat features could prevent formation of large groups due to the difficulty of maintaining group cohesion on steep, rugged terrain. Warrick and Krausman (1987) found group size of sheep from two populations in Arizona increased as ruggedness decreased (e.g., as animals moved away from escape terrain). Sheep formed larger groups, and maintained high levels of vigilance, when moving away from escape terrain to enter washes on the flats to feed on blue paloverde and ironwood trees.

**Summary**

The large-scale hypothesis of an optimal or adaptive response of vigilance in populations of desert bighorn ewes under different predation risk was rejected. There was no difference in mean vigilance between bighorn sheep populations in habitat with low versus high predation risk. These results, based on replicated samples of six populations, contrast with other, less extensive studies of ungulate vigilance behavior and were inconsistent with the predictions of an optimal allocation of time to vigilance and foraging. Plastic adjustments of vigilance in response to group size and terrain variables were consistent with optimal and adaptive predictions in habitat with predation risk from mountain lions.

In the following chapter, I examine norms of reaction for vigilance of the three native bighorn sheep populations inhabiting low-elevation mountain ranges without resident mountain lions to determine whether vigilance behavior in these populations reflects predicted patterns of adaptive behavioral plasticity in vigilance due to the costs of maintaining vigilance in the absence of predators. In Chapter 4, I compare changes in
vigilance in populations translocated at different intervals of time from habitat under relaxed predation into habitat with mountain lions.

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CHAPTER 3

VIGILANCE IN NATIVE DESERT BIGHORN SHEEP POPULATIONS: RESPONSE TO RELAXED SELECTION

Abstract

Antipredator behaviors such as vigilance are often costly because they prevent investment in other activities, such as feeding, resting, or looking for mates. When changes in predation regimes result in isolation of prey from predators, these formerly adaptive antipredator behaviors can be lost. The loss may be partial, may occur over evolutionary time as a response to relaxed selection, or may occur within an individual’s lifetime through learning. I compared mean vigilance and mean norms of reaction for vigilance expressed across group size and terrain type of three native bighorn sheep populations inhabiting low-elevation mountain ranges without resident mountain lions to determine whether vigilance behavior in these populations reflects predicted patterns of optimal or adaptive behavioral plasticity in vigilance due to the costs of maintaining vigilance in the absence of predators. The predictive hypothesis was that overall mean vigilance would be relatively low and the relationship between vigilance, group size, and terrain type would be weak or non-existent (a slope of zero) due to the costs of maintaining vigilance in the absence of predators.
Results of the comparisons showed that populations differed significantly in their response to the absence of large predators. Vigilance in the River Mountain population resembled predicted patterns of a response to relaxed selection. Mean vigilance in this population was the lowest of the three sheep populations and the mean norm of reaction for vigilance expressed across group size and terrain type was flat, indicating that these ewes did not adjust vigilance in response to either of these environmental cues.

Total mean vigilance and mean norms of reaction for vigilance of sheep in the Eagle Mountain population suggested a partial response to relaxed selection. Mean vigilance was relatively high, but the mean norm of reaction expressed across group size and terrain type was flat. In the Muddy Mountains, the relationship between vigilance and group size was negative for ewes foraging on escape terrain but positive for ewes foraging more than 100 meters away from escape terrain.

The persistence of high mean vigilance in both the Muddy and Eagle Mountain populations, and the nonadaptive plastic response of vigilance to group size and terrain type in the Muddy Mountain population resulted in behavioral variance among populations in low predation risk habitat that contributed to the lack of large-scale divergence of vigilance behavior observed in Chapter 2.

Introduction

Predation is a strong selective force in the evolution of antipredator adaptations (Lima and Dill 1990). Therefore, differences in predation regimes should cause geographic differences in antipredator behavior (Coss 1999; Magurran 1999). These differences can arise when populations invade new habitats lacking a class of predators that were
abundant in the environment of the source population (Coss 1999), or when historic predators, such as wolves and grizzly bears, have been extirpated from a region (Berger 1999). Populations may then experience relaxed selection on specific behavioral phenotypes (e.g., Curio 1975; Pressley 1981; Coss 1999; Berger et al. 2001). For example, caribou (Rangifer rangifer) in Alaska are sympatric with wolves (Canis lupus) and vigilance (scanning for predators) in these populations is much higher than for conspecifics from western Greenland where wolves have been absent for 4,000 years (Boving and Post, 1997). Under relaxed selection, traits may fragment when mutations that cause loss of a phenotype are not at a selective disadvantage (Coss 1999). Examples have been found for a number of species, including birds (Cruz and Wiley 1989; Davies and Brooke 1989), deer mice (Kavaliers 1990, Korth 1994), ground squirrels (Owings and Coss 1977, Coss et al. 1993) and fish (Foster and Ploch 1990).

Behavioral responses to relaxed selection can be somewhat unpredictable, and in many cases, it may be difficult to determine whether relaxed selection has actually occurred. Behavioral characters can be retained for long periods of time after selection has been relaxed and traits can be retained though phylogenetic inertia, parallel directional selection, or low heritability (Coss 1999; Kaneshiro 1989). Retention of a behavioral response may reflect evolutionary persistence of an historical adaptation (Pressley 1981; Thompson 1990) or the trait may be retained as a result of parallel directional selection in response to the presence of a predator in the novel habitat (Pressley 1981). Coss (1999) found members of populations of California ground squirrels to retain the ability to discriminate rattlesnakes and gopher snakes despite relaxed selection for a time period spanning an estimated 70,000-300,000 years.
Retention of these characters was attributed to low heritability for the trait through time in the population subject to relaxed selection (Mousseau and Roff 1987).

**Vigilance**

Vigilance is a phenotypically plastic trait that is directly and indirectly linked to fitness (Elgar 1989; Lima and Dill 1990). Less vigilant individuals are more vulnerable to predation than their conspecifics (Fitzgibbon 1989; Scheel 1993) however, as individual vigilance increases foraging efficiency decreases, which can lower energy intake (Stephens and Krebs 1986; Lima and Dill 1990). If total energy intake is an important determinant of fitness, animals can be predicted to behave in a manner that maximizes their net rate of energy intake while at the same time minimizing predation risk by adjusting the amount of time spent in foraging verses antipredator activities.

Models describing optimal vigilance assume natural selection, and most models assume there will be enough phenotypic variation and additive genetic variation in a population to result in an optimal solution (within constraints) that maximizes fitness (Pulliam et al. 1982; Lima 1987; Packer and Abrams 1990; McNamara and Houston 1992; Parker and Smith 1990; but see Mangel 1991 and Pierce and Ollason 1987). Animals may also, adjust their behavior through adaptive phenotypic plasticity (Piggliucci 2001) such that natural selection yields an optimal mean norm of reaction across environments. Behavioral change can also be the result of non-genetic cultural transmission, which could increase an individual’s fitness during its lifetime (Papaj 1994). For purposes of this study, the term adaptive will be used in a broad sense to describe behavioral phenotypes that match expectations of optimal models and may confer high fitness. An optimal level of vigilance (generally quantified as the amount of...
time an animal spends looking with head up during a foraging bout) should occur when there is a “perfect” tradeoff between food gain and predator avoidance (Pulliam et al. 1982; Stephens and Krebs 1986; Lima and Dill 1990.

**Norms of Reaction**

Behavioral phenotypes are the result of a complex combination of individual differences in genes affecting behavior and in experiential environments that can be expressed as norms of reaction (Pigliucci 2001). The norm of reaction for a genotype is the set of different behavioral phenotypes predictably expressed in response to the environments that an individual encounters. Environmental variation in cues affecting behavior can be both spatial and temporal (Gomulkiewicz and Kirkpatrick 1992; Thompson 1999). Examples of the use of norms of reaction to study population-specific behavioral phenotypic plasticity can be found in Carroll and Corneli (1999), Ehlinger (1999), and Thompson (1999).

A number of studies have shown that vigilance behavior varies in response to local environmental factors that affect predation risk (Berger 1978; Lipetz and Beckoff 1982; Underwood 1982; Berger 1991; Bednekoff and Ritter 1994; Frid 1997; Burger and Gochfeld 1988; Burger et al. 2000). Thus, for a population of bighorn sheep inhabiting a particular mountain range, the mean norm of reaction for vigilance is described by the set of phenotypic means expressed by individuals in the population over a range of environmental variables such as habitat type or group size. This population norm of reaction would be adaptive if the differential expression of the behavior in different environments confers high fitness to individual sheep.
Population Variation in Vigilance: Absence of Large-Scale Adaptation

In Chapter Two, I tested the hypothesis that differences in vigilance between desert bighorn sheep populations in regions with predators and regions without predators reflect predicted patterns of optimal or adaptive behavior. I assumed individual vigilance was a plastic trait and tested for population divergence in norms of reaction expressed across group size and terrain. Sheep populations in habitats without resident mountain lions were native populations. Populations under high predation risk, in habitats with mountain lions, that had originally been translocated from a mountain range uninhabited by mountain lions. Time since translocation ranged from two to approximately twenty years.

I predicted that bighorn sheep populations in low-elevation mountain ranges uninhabited by mountain lions would have low levels of vigilance due to the costs of maintaining vigilance in the absence of predators. The lack of consistently higher vigilance in populations under high predation risk compared to populations under low predation risk led me to reject the large-scale hypothesis that bighorn sheep would show adaptive differences in vigilance when inhabiting regions with and without large predators. However, I also tested hypotheses about the covariation of vigilance with environmental factors that affect perceived predation risk, such as group size and location with respect to escape terrain. These results revealed plastic adjustments of vigilance in response to group size and terrain variables for sheep populations that are consistent with adaptive predictions for populations with predation risk from mountain lions. In contrast, mean vigilance averaged across three populations of sheep inhabiting low-elevation desert mountain ranges did not covary with group size or escape terrain.
In this chapter and the next I address population differences in vigilance in the presence and absence of mountain lions to determine the conditions that have prevented large-scale adaptation. Here, I examine norms of reaction for vigilance of the three native bighorn sheep populations inhabiting low-elevation mountain ranges without resident mountain lions to determine whether vigilance behavior in these populations reflects predicted patterns of adaptive behavioral plasticity in vigilance due to the costs of maintaining vigilance in the absence of predators. In chapter 4, I compare changes in vigilance in populations of sheep transplanted at different intervals of time into habitat occupied by mountain lions to determine whether populations under relaxed predation pressure retain enough adaptive plasticity to adjust vigilance behavior in response to increased predation risk.

**Hypotheses for Relaxed Selection**

The lack of significant divergence in overall mean vigilance of the three replicate populations in low-elevation mountain regions compared to the three replicate populations in high-elevation mountain regions could be due to high variance of vigilance among populations within low-elevation mountain ranges and persistence of vigilance despite relaxed selection, or it could be due to the lack of adaptation and lack of evolution of increased vigilance in the populations translocated to high-elevation mountain ranges with predators.

For example, if selection favors increased foraging efficiency then an individual should adjust foraging behavior to maximize the amount of time spent feeding and reduce time spent being vigilant. If selection to increase foraging efficiency is low, the cost of vigilance would be low and there should be little selection to decrease the amount of time
spent vigilant. Thus, if there is a cost to vigilance for bighorn sheep populations without resident mountain lions, among-population variance would be low. If the cost of vigilance differs among populations as a result of historical patterns or differences in forage quality among mountain ranges, among-population variance should be high. Alternatively, variance among populations would be predicted to vary randomly if evolution of vigilance were due to genetic drift or selection on a correlated trait.

Under relaxed predation, evolution of reduced vigilance will depend on the intensity of natural selection on foraging traits that are linked to vigilance through time trade-offs. If an optimal level of vigilance is maintained by natural selection it can be predicted that due to the cost of vigilance (i.e., a decrease in foraging efficiency), populations in habitats with low predation risk will have adjusted their vigilance to maximize foraging efficiency. The predictive hypothesis for adaptive plasticity in vigilance due to the costs of maintaining vigilance in the absence of predators was that both mean vigilance and among-population variance in vigilance would be relatively low. In addition, if there is no benefit from vigilance in the absence of predators and natural selection acts to increase foraging time (i.e. efficiency), bighorn sheep would have no plasticity in vigilance in response to environmental covariates and vigilance norms of reaction would be flat and invariant. Alternatively, if the cost of vigilance differs among populations as a result of historical patterns or differences in forage quality among mountain ranges, among-population variance would be high and some populations might maintain high mean vigilance and adaptive plasticity in vigilance with respect to ecological covariates. Other alternative hypotheses are that there would be random divergence among populations due to genetic drift, or correlated responses to selection of unknown traits.
Methods and Analysis

Study Sites

Vigilance behavior was sampled from three populations of desert bighorn sheep located in low-elevation mountain ranges in the Mojave Desert. These ranges were the River and Muddy Mountains in Clark County, Nevada, and Eagle Mountain in Riverside County, California (Figure 1, Chapter 2). Vegetation in these low-elevation mountain ranges is typical desert shrub with some xero-riparian species found in the washes (Bradley and Deacon 1965). All three mountain ranges are uninhabited by resident mountain lions, although occasionally, migrant lions have been sighted in the Muddy and River Mountains (Leslie and Douglas 1979; pers. comm. Ross Haley). Smaller predators, such as coyotes and golden eagles, are present in all mountain ranges (Leslie and Douglas 1979; Divine 1998).

Sampling Methods

Behavioral data were collected from bighorn sheep in the River Mountains during 1987 and 1988. Data from the Eagle and Muddy Mountain populations were collected from 1995 through 2000. Vigilance levels were quantified as the proportion of time during a foraging bout that an animal stopped feeding to raise its head above the shoulders and look around at the surrounding terrain. Vigilance behavior of bighorn sheep was observed and recorded using a combination of focal animal and scan sampling techniques (Altmann 1974). To eliminate variance associated with differences between ewe and ram behavior, data were collected from ewes only. Ewes were also selected because they are subject to a higher proportion of deaths due to predation than are rams (Berger 1991). Records were made of location, distance from the base of the nearest
mountainside or rugged cliff (termed "escape terrain"), vegetation type within 2 meters, adult group size, and composition. Once a group of sheep were located and > 60% of the animals were feeding, a focal animal was randomly selected and observed continuously for 5 minutes (300 sec). Sheep were observed with a Celestron C-5 telescope (90 power) and could be easily seen from over one half mile. Data were only collected on animals that were unaware of my presence and I made an effort to collect data from as far from the animals as possible.

Observations were only made on sheep that did not show signs that they had observed me. If animals were observed looking directly towards me in a non-random fashion, I did not collect behavioral data from them. All behavioral activities were recorded continuously into a tape recorder. A focal animal was defined as vigilant when it lifted its head to shoulder height and surveyed its surroundings. Following the focal animal sample, another ewe was randomly chosen, excluding the previous animal until all members of the group had been observed. No attempt was made to discriminate between 'active' verses 'weak' vigilance (Alados, 1985), determine whether vigilance was directed at specific objects (see LaGory, 1986), or whether sheep were engaged in decision-making concerning moving to other foraging patches (e.g. in buffalo; Prins 1996). Instead, I assumed that ewes were using the head-up posture to gather information on all possible factors. If animals were observed looking directly towards me in a non-random fashion, I did not collect behavioral data because I was interested in the overall, or general vigilance maintained in each population and not the response of ewes to a human observer. In addition, it is also possible that, depending on their degree of acclimation to humans, a population of sheep may react less alarmingly to a human
observer than to a potential predator. Behavioral data were transcribed using a stopwatch to measure scan durations to the nearest second and enable calculation of the proportion of time spent vigilant.

**Statistical Analysis**

To test the hypotheses of an adaptive phenotypic response to mitigate the cost of vigilance in habitat without large predators, mean vigilance and norms of reaction for vigilance expressed across group size and relation to escape terrain were compared between sheep populations using analysis of covariance and followed the technique described in Littell et al. (2001). The technique is discussed in detail in Chapter Two. Bighorn sheep population and relation to escape terrain (areas on, or < 100 meters from cliffs or steep, rocky slopes (escape terrain) versus non-escape terrain; areas > 100 meters from cliffs or steep, rocky slopes) were considered main effects and group size was treated as a covariate. Categories for distance from escape terrain were based upon Berger (1991). Prior to the analysis, vigilance was arcsine transformed to meet assumptions of normality and homogeneity of variance (Zar 1999). The assumption of homogeneous variance was evaluated with a plot of the residuals versus the estimated treatment means. Residuals were examined to verify normality and used to provide visual evaluations of the analysis of variance assumptions for homogeneous variances and normal distribution of experimental errors.

**Results**

Mean vigilance during foraging bouts of sheep in Eagle Mountain (19.6% ± 1.6 S.E., n = 92, range 0.0 to 70.70%) and the Muddy Mountains (18.8 ± 1.9 S.E., n = 67,
range 0 to 79.7%), was nearly twice higher than vigilance of sheep in the River
Mountains (9.9% ± 0.7, S.E., n = 133 range 0.0 to 30.0%). Mean group size was largest
for ewes in the River Mountains, where group size averaged 8 adult sheep (median = 6.0;
n = 81, range 2 to 30). Mean group size in the Eagle Mountain population was 6 (median
= 4.5; n = 36) and ranged from 1 to 26. Group size of sheep in the Muddy Mountains
ranged from 1 to 16 animals with an average of 6 individuals per group (median = 5.0;
total number of groups = 11). The Kruskal-Wallis Test (Zar 1999) was used to compare
median group size between the three populations because group size data were non-
normal even after log transformation. Median group size of sheep from the River
Mountains population was significantly higher than that of the Eagle Mountain
population ($H_{0.05, 36,11,81} = 6.76, P = 0.034$). Linear regressions describing the relationship
between group size and vigilance for the three bighorn sheep populations are illustrated
in Figure 5. The slope of the relationship of group size on vigilance for bighorn ewes in
both the Muddy and River Mountains did not differ significantly from zero (Table 4).
These results are consistent with predictions of adaptive adjustments in mean vigilance
for populations under relaxed selection (slope, $\beta$, of the relationship would equal zero).
In the Eagle Mountain population, the relationship of group size and vigilance of ewes
was characterized by a relatively weak but significant negative slope (regression
coefficient = 5.996, $\beta = -0.449$, $P = 0.019$), results that are inconsistent with predictions of
behavior under relaxed selection.

**Determining the Form of the Covariate in the Model**

Results of the slopes-equal-to-zero model for the analysis of covariance, showed a
significant group-size-by-population-by-escape terrain interaction ($F_{8,359} = 2.22; P$
Figure 5. Linear regressions showing the effect of group size on vigilance of three populations of desert bighorn sheep inhabiting low-elevation mountain ranges in the Mojave Desert. All three mountain ranges are uninhabited by resident mountain lions.
Table 4  Regression statistics for group size and proportion of time spent vigilant during foraging bouts for three bighorn sheep populations in habitat without resident mountain lions (t-test slope = 0).

<table>
<thead>
<tr>
<th>Population</th>
<th>Regression Coefficient</th>
<th>Standard Error</th>
<th>t Statistic</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eagle Mountain</td>
<td>-0.442 ±0.184</td>
<td>-2.395</td>
<td>0.019</td>
<td></td>
</tr>
<tr>
<td>Muddy Mountains</td>
<td>-0.551 ±0.337</td>
<td>-1.635</td>
<td>0.106</td>
<td></td>
</tr>
<tr>
<td>River Mountains</td>
<td>-0.044 ±0.039</td>
<td>-0.162</td>
<td>0.263</td>
<td></td>
</tr>
</tbody>
</table>

=0.026), indicating that the slopes and intercepts are not all equal to zero and that group size should be included as a covariate in the model. The equal slopes hypothesis was also rejected due to a significant group-size-by population interaction (F3,362 =2.66, P= 0.048), signifying that the relationship between group size and vigilance was not the same across all populations.

Population Mean Vigilance

To test the hypothesis of an adaptive behavioral response of bighorn sheep to relaxed predation, a multiple comparison procedure was performed using the unequal slopes model. Mean vigilance was compared at low (4), medium (9), and high (14), group sizes (Table 5). These values were chosen to include a range of group sizes that would fit all populations in the analysis. Results of the contrasts showed that at all three group size values, adjusted mean vigilance of bighorn sheep in the River Mountains was significantly lower than adjusted mean vigilance on Eagle Mountain. Adjusted mean vigilance of sheep foraging in the Muddy Mountains was intermediate between the other
two mountain ranges, but the difference was not significant from either population (Table 5).

Norms of Reaction for Vigilance Expressed Across Group Size and Terrain

Regression coefficients for linear relationships between group size and proportion of time spent vigilant in relation to escape terrain are shown in Table 6. In the Eagle and River Mountains, norms of reaction for vigilance in response to group size matched that of predicted responses under relaxed selection. The slope of the relationships for the effect of either terrain category (on or near escape terrain versus away from escape terrain) on vigilance did not differ from zero in these populations. In the Muddy Mountains, the slope of the relationships were not equal to zero, there was a negative correlation between group size and vigilance when sheep foraged on or near escape terrain, but when sheep foraged more than 100 meters away from escape terrain, the slope was positive (Table 6). These results do not match predictions for group size effects on vigilance under conditions of high predation risk or under relaxed selection and suggest that ewes in this population may be exhibiting nonadaptive behavior when foraging under conditions of greatest predation risk.

Multiple comparisons were used to compare vigilance in relation to escape terrain for each population at group sizes 4, 9, and 14 and to obtain adjusted means for combinations of population, and relation to escape terrain (Figure 6). Neither the River Mountains nor Eagle Mountain populations displayed differences in vigilance between terrain types at the selected group sizes (Table 7). In the Muddy Mountains, however, adjusted mean vigilance of small groups of sheep foraging on or near escape terrain was significantly higher than vigilance of ewes foraging away from escape terrain ($P = 0.052$). The results
Table 5. Results of the comparisons of main effects for mean vigilance between populations of bighorn sheep in habitat without resident mountain lions across all terrain types. Adjusted mean vigilance was compared at three group size values from each of the different regression models. Degrees of freedom were determined using the Satterwaite approximation.

<table>
<thead>
<tr>
<th>Contrasts for Main Effects (Populations)</th>
<th>Covariate value (Group size)</th>
<th>Adjusted Mean (± SE) Eagle Mtns</th>
<th>Adjusted Mean (± SE) Muddy Mtns</th>
<th>t Value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eagle Mtn. vs. Muddy Mtns.</td>
<td>4</td>
<td>27.5 (±2.4)</td>
<td>19.3 (±4.7)</td>
<td>1.63</td>
<td>0.104</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>25.1 (±1.8)</td>
<td>18.7 (±3.3)</td>
<td>1.58</td>
<td>0.115</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>22.6 (±2.1)</td>
<td>18.2 (±3.7)</td>
<td>1.49</td>
<td>0.138</td>
</tr>
<tr>
<td>Eagle Mtn. vs. River Mtns.</td>
<td>4</td>
<td>27.5 (±2.4)</td>
<td>16.7 (±1.7)</td>
<td>-2.67</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>25.1 (±1.8)</td>
<td>15.4 (±1.9)</td>
<td>-4.82</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>22.6 (±2.1)</td>
<td>14.1 (±3.3)</td>
<td>-2.67</td>
<td>0.008</td>
</tr>
<tr>
<td>Muddy Mtns. vs. River Mtns.</td>
<td>4</td>
<td>19.3 (±4.7)</td>
<td>16.7 (±1.7)</td>
<td>-0.17</td>
<td>0.862</td>
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<tr>
<td></td>
<td>9</td>
<td>18.7 (±3.3)</td>
<td>15.4 (±1.9)</td>
<td>0.02</td>
<td>0.983</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>18.2 (±3.7)</td>
<td>14.2 (±3.3)</td>
<td>0.19</td>
<td>0.853</td>
</tr>
</tbody>
</table>
Table 6. Relationship between group size and proportion of time spent vigilant in relation to escape terrain for bighorn sheep populations in mountain ranges without resident mountain lions (t test slope = 0). Vigilance data were arcsine transformed prior to the analysis.

<table>
<thead>
<tr>
<th>Population</th>
<th>Regression Coefficient</th>
<th>Standard Error</th>
<th>t Statistic</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>On or less than 100 meters from escape terrain</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eagle Mountain</td>
<td>-0.414 ± 0.222</td>
<td>-1.863</td>
<td>0.066</td>
<td></td>
</tr>
<tr>
<td>Muddy Mountains</td>
<td>-1.274 ± 0.567</td>
<td>-2.246</td>
<td>0.029</td>
<td></td>
</tr>
<tr>
<td>River Mountains</td>
<td>-0.501 ± 0.605</td>
<td>-0.828</td>
<td>0.415</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Greater than 100 meters from escape terrain</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eagle Mountain</td>
<td>-0.563 ± 0.354</td>
<td>-1.589</td>
<td>0.130</td>
<td></td>
</tr>
<tr>
<td>Muddy Mountains</td>
<td>1.0585 ± 0.135</td>
<td>3.363</td>
<td>0.008</td>
<td></td>
</tr>
<tr>
<td>River Mountains</td>
<td>-0.019 ± 0.118</td>
<td>-0.162</td>
<td>0.871</td>
<td></td>
</tr>
</tbody>
</table>

of these comparisons do not match predictions of adaptive vigilance behavior under conditions of high predation risk nor under relaxed selection.

Differences in Norms of Reaction for Vigilance Among Populations

Results of the multiple contrasts of adjusted means for vigilance of the three bighorn sheep populations expressed across group size and relation to escape terrain showed significant differences among populations, indicating that ewe response to relaxed predation was not similar across all populations (Figure 8). When foraging away from escape terrain, ewes on Eagle Mountain were always more vigilant than ewes in the River Mountains, regardless of group size (Table 8). In the Muddy Mountains, adjusted means for vigilance of all group sizes foraging away from escape terrain were intermediate.
between ewes in the Eagle and River Mountains, and did not differ significantly from either population.

When foraging on or near escape terrain, ewes foraging in small and medium sized groups in the Eagle and Muddy Mountains were more vigilant than ewes foraging under similar circumstances in the River Mountains (Table 9). Sheep foraging in large groups were more vigilant in the Eagle Mountain population than the River Mountains (P = 0.059). While vigilance of large ewe groups foraging on or near escape terrain in the Muddy Mountains was intermediate to the Eagle Mountain and River Mountains populations, these results suggest that variance in the patterns of vigilance among populations contributed to the absence of large-scale divergence of vigilance in response to differences in predation regimes.

Discussion

In this chapter, I address differences in vigilance among bighorn sheep populations in the absence of mountain lions to determine the conditions that have contributed to the lack of large-scale adaptation of vigilance in response to differences in predation risk (Chapter 2). The lack of a significant difference in total mean vigilance of the three replicate populations in habitat without resident mountain lions compared to the three replicate populations from regions subject to lion predation was predicted to result from some combination of (1) high variance of vigilance among populations within low-elevation mountain ranges, (2) persistence of high vigilance despite relaxed selection or by lack of adaptation, and (3) lack of evolution of increased vigilance in the translocated populations occupying high-elevation mountain ranges (Chapter 4).
Figure 6. Mean norms of reaction for vigilance in relation to group size and escape terrain for three populations of desert bighorn ewes in habitat without resident mountain lions. Terrain types were areas on, or less than 100 meters nearest cliffs or steep, rocky slopes (escape terrain) and areas greater than 100 meters from nearest cliffs or steep, rocky slopes (non-escape terrain). Lines connecting means are not regression lines. Matching letters are adjusted means that differed significantly from one another ($P = 0.052$). Vertical lines are standard error bars.
Table 7. Results of the comparisons between terrain types for adjusted mean vigilance of bighorn sheep foraging in habitat without resident mountain lions. Terrain types were areas on, or less than 100 meters nearest cliffs or steep, rocky slopes (escape terrain) and areas greater than 100 meters from nearest cliffs or steep, rocky slopes (non-escape terrain). Adjusted mean vigilance was compared at three group size values from each of the different regression models. Degrees of freedom were determined using the Satterwaite approximation.

<table>
<thead>
<tr>
<th>Contrasts for Main Effects</th>
<th>Covariate value (Group size)</th>
<th>Adjusted Mean (± SE) Escape terrain</th>
<th>Adjusted Mean (± SE) Non-Escape Terrain</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>River Mountains</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terrain 1 vs Terrain 2</td>
<td>4</td>
<td>16.5 (±2.2)</td>
<td>16.9 (±1.3)</td>
<td>0.871</td>
</tr>
<tr>
<td>Terrain 1 vs. Terrain 2</td>
<td>9</td>
<td>20.3 (±1.2)</td>
<td>21.7 (±2.4)</td>
<td>0.340</td>
</tr>
<tr>
<td>Terrain 1 vs. Terrain 2</td>
<td>14</td>
<td>18.1 (±1.5)</td>
<td>21.2 (±2.4)</td>
<td>0.354</td>
</tr>
<tr>
<td><strong>Eagle Mountains</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terrain 1 vs. Terrain 2</td>
<td>4</td>
<td>26.5 (±1.5)</td>
<td>28.5 (±3.3)</td>
<td>0.597</td>
</tr>
<tr>
<td>Terrain 1 vs. Terrain 2</td>
<td>9</td>
<td>24.5 (±1.2)</td>
<td>25.6 (±2.2)</td>
<td>0.661</td>
</tr>
<tr>
<td>Terrain 1 vs. Terrain 2</td>
<td>14</td>
<td>22.4 (±1.6)</td>
<td>22.8 (±2.5)</td>
<td>0.883</td>
</tr>
<tr>
<td><strong>Muddy Mountains</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terrain 1 vs. Terrain 2</td>
<td>4</td>
<td>27.1 (±1.6)</td>
<td>11.5 (±7.8)</td>
<td>0.052</td>
</tr>
<tr>
<td>Terrain 1 vs. Terrain 2</td>
<td>9</td>
<td>20.7 (±2.1)</td>
<td>16.8 (±4.4)</td>
<td>0.430</td>
</tr>
<tr>
<td>Terrain 1 vs. Terrain 2</td>
<td>14</td>
<td>22.1 (±3.1)</td>
<td>14.3 (±4.3)</td>
<td>0.145</td>
</tr>
</tbody>
</table>
Figure 7. Comparison of mean norms of reaction for vigilance expressed across group size and location in relation to escape terrain for three populations of desert bighorn sheep inhabiting low-elevation mountain ranges without resident mountain lions. Terrain types were areas on, or less than 100 meters, from nearest cliffs or steep, rocky slopes (escape terrain) and areas greater than 100 meters from nearest cliffs or steep, rocky slopes (non-escape terrain). Lines connecting means are not regression lines. See Table 9 for significant differences among adjusted means.
Table 8. Results of the multiple comparisons for mean vigilance between populations of bighorn sheep ewes foraging away from escape terrain (> 100 m) in habitat without resident mountain lions. Adjusted mean vigilance was compared at three group size values from each of the different regression models. Degrees of freedom were determined using the Satterwaite approximation.

<table>
<thead>
<tr>
<th>Contrasts for Main Effects (Populations)</th>
<th>Covariate value (Group size)</th>
<th>Adjusted Mean (± SE) Eagle Mtns</th>
<th>Adjusted Mean (± SE) Muddy Mtns</th>
<th>t Value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Away from Escape Terrain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eagle Mtn. vs. Muddy Mtns</td>
<td>4</td>
<td>28.5 (±3.3)</td>
<td>11.5 (±7.8)</td>
<td>2.01</td>
<td>0.046</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>25.6 (±2.4)</td>
<td>16.8 (±4.4)</td>
<td>1.76</td>
<td>0.080</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>22.8 (±2.5)</td>
<td>22.1 (±3.1)</td>
<td>0.19</td>
<td>0.849</td>
</tr>
<tr>
<td>Eagle Mtn. vs. River Mtns</td>
<td>4</td>
<td>28.5 (±3.3)</td>
<td>16.9 (±1.3)</td>
<td>-3.25</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>25.6 (±2.4)</td>
<td>16.8 (±1.0)</td>
<td>-3.37</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>22.8 (±2.5)</td>
<td>16.7 (±1.1)</td>
<td>-2.22</td>
<td>0.027</td>
</tr>
<tr>
<td>Muddy Mtns vs. River Mtns</td>
<td>4</td>
<td>11.5 (±7.8)</td>
<td>16.9 (±1.3)</td>
<td>0.39</td>
<td>0.491</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>16.8 (±4.4)</td>
<td>16.8 (±1.0)</td>
<td>0.01</td>
<td>0.991</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>22.1 (±3.1)</td>
<td>16.7 (±1.2)</td>
<td>-1.60</td>
<td>0.120</td>
</tr>
</tbody>
</table>
Table 9. Results of the multiple comparisons for mean vigilance between populations of bighorn sheep ewes foraging on or near escape terrain (<100 m) in habitat without resident mountain lions. Adjusted mean vigilance was compared at three group size values from each of the different regression models. Degrees of freedom were determined using the Satterwaite approximation.

<table>
<thead>
<tr>
<th>Contrasts for Main Effects (Populations)</th>
<th>Covariate value (Group size)</th>
<th>Adjusted Mean (± SE) Eagle Mtns</th>
<th>Adjusted Mean (± SE) Muddy Mtns</th>
<th>t Value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>On or Near Escape Terrain</td>
<td>Eagle Mtns</td>
<td>Muddy Mtns</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eagle Mtn. vs. Muddy Mtns</td>
<td>4</td>
<td>26.5 (±1.5)</td>
<td>27.0 (±1.6)</td>
<td>-0.22</td>
<td>0.823</td>
</tr>
<tr>
<td>Eagle Mtn. vs. Muddy Mtns</td>
<td>9</td>
<td>24.5 (±1.2)</td>
<td>20.7 (±2.1)</td>
<td>1.59</td>
<td>0.114</td>
</tr>
<tr>
<td>Eagle Mtn. vs. Muddy Mtns</td>
<td>14</td>
<td>22.4 (±1.6)</td>
<td>14.3 (±4.3)</td>
<td>1.76</td>
<td>0.080</td>
</tr>
<tr>
<td>Eagle Mtn. vs. River Mtns</td>
<td>4</td>
<td>26.5 (±1.5)</td>
<td>16.5 (±2.2)</td>
<td>-3.83</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Eagle Mtn. vs. River Mtns</td>
<td>9</td>
<td>24.5 (±1.2)</td>
<td>14.0 (±2.8)</td>
<td>-3.46</td>
<td>0.001</td>
</tr>
<tr>
<td>Eagle Mtn. vs. River Mtns</td>
<td>14</td>
<td>22.4 (±1.6)</td>
<td>11.5 (±5.5)</td>
<td>-1.90</td>
<td>0.059</td>
</tr>
<tr>
<td>Muddy Mtns. vs. River Mtns</td>
<td>4</td>
<td>27.0 (±1.6)</td>
<td>16.5 (±2.2)</td>
<td>-3.89</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Muddy Mtns. vs. River Mtns</td>
<td>9</td>
<td>20.7 (±2.1)</td>
<td>14.0 (±2.8)</td>
<td>-1.91</td>
<td>0.057</td>
</tr>
<tr>
<td>Muddy Mtns. vs. River Mtns</td>
<td>14</td>
<td>14.3 (±4.3)</td>
<td>11.5 (±5.5)</td>
<td>-0.40</td>
<td>0.692</td>
</tr>
</tbody>
</table>
Here, I examined norms of reaction for vigilance of the three native bighorn sheep populations inhabiting low-elevation mountain ranges without resident mountain lions to determine whether behavior in these populations reflects predicted patterns of adaptive behavioral plasticity due to the costs of maintaining vigilance in the absence of predators. Based on predictions from optimal foraging theory (Stephens and Krebs 1986; Charnov 1976; Pyke et al. 1977) I predicted that if natural selection in an environment with low predation risk favors increased foraging efficiency, individuals will adjust foraging behavior to maximize the amount of time spent feeding and reduce the amount of time spent vigilant. The relationship between vigilance and its environmental covariates would be weak or nonexistent as there would be no benefit to adjusting vigilance in the absence of predators. Based on these predictions, bighorn ewes from populations that inhabit low-elevation mountain ranges without resident mountain lions were predicted to lower the cost of vigilance through a decrease in mean vigilance and weakening of mean norms of reaction expressed across group size and relation to escape terrain.

Response to Relaxed Predation

Results indicate that not all bighorn sheep populations sampled from habitat without resident mountain lions exhibited predicted optimal or adaptive responses to relaxed predation. Only sheep from the River Mountains population exhibited vigilance phenotypes that fit predicted adaptive patterns of a response to relaxed selection. Ewes in this population had the lowest mean vigilance of the three populations sampled. Mean vigilance was nearly half that of the Eagle and Muddy Mountain populations, although this difference in means was only significant for the Eagle Mountain population. Additionally, ewes in the River Mountains did not adjust vigilance in response to group
size or in relation to escape terrain. Mean norms of reaction for vigilance expressed across group size and escape terrain were flat.

The pattern of vigilance behavior of ewes in Eagle Mountain suggests that this population has evolved a partial response to relaxed selection. Ewes from this population had the highest level of mean vigilance of all three replicate populations, a level that is inconsistent with predictions of an adaptive response to natural selection for a decrease in vigilance. Instead, ewes maintained a level of vigilance that was consistent with expected levels in habitat with high predation risk. However, sheep from the Eagle Mountain population did exhibit norms of reaction expressed across group size and escape terrain that were flat, and as predicted under the hypothesis of relaxed selection.

Patterns of vigilance behavior within the Muddy Mountains are highly variable and do not match optimal or adaptive predictions. Total mean vigilance in the Muddy Mountains was relatively high, results that were inconsistent with a response to relaxed selection. Norms of reaction for vigilance expressed across group size and escape terrain indicate that plastic response of vigilance are highly variable with respect to environmental cues. There was a significant relationship between group size and vigilance for sheep foraging across terrain types, but when this relationship was examined within terrain types, some plastic responses of vigilance were opposite to predictions of optimal behavior. Adjusted mean vigilance of small groups of ewes foraging on or near escape terrain was significantly higher than vigilance of small ewe groups foraging away from escape terrain. Thus, under conditions of highest perceived predation risk (small groups foraging away from escape terrain) ewes had the lowest vigilance levels.
Possible Mechanisms for the Persistence of Vigilance

Factors that could cause the observed responses to relaxed selection in the absence of predators include low or no cost to vigilance in terms of trade-offs with other traits, historical contingencies, evolutionary persistence of a historical adaptation through learned or culturally transmitted behavior, genetic constraints, phylogenetic inertia, and selection on correlated characters (Arnold 1994; Coss 1999; Magurran 1999; Reichert 1999). The apparent partial response to relaxed selection in the Eagle Mountain population could be attributed to a number of these factors. The flat norm of reaction for vigilance expressed across group size and terrain type suggests that in this mountain range there could be a cost to vigilance through foraging tradeoffs.

Although mountain lions are not considered permanent residents in mountain ranges uninhabited by deer, there are rare sightings of lions in low-elevation ranges in southern Nevada (based on reports to the Nevada Division of Wildlife, Pat Cummings, pers. comm. 2003) and it is possible that ewes in these populations experience a minimal amount of predation from occasional lions to offset the cost to vigilance in loss of foraging time. The high level of vigilance, inconsistent with predictions of an adaptive response to relaxed predation, suggests that there is also some selection to maintain vigilance. High mean vigilance could be maintained as a result of selection due to predation by smaller resident predators such as coyotes, although these mostly prey on lambs and yearling sheep (Sawyer and Lindzey 2002). High mean vigilance could also be attributed to possible predation by non-resident mountain lions that occasionally move through low-elevation desert ranges, although the River Mountain population, which has
a pattern of vigilance that matches predicted adaptive responses to relaxed selection, is also subject to rare visits by lions (Leslie and Douglas 1979).

If high a level of vigilance is not maintained through selection as a result of smaller resident predators and/or rare visits by mountain lions, it could be caused by retention of the trait as a learned response and could have been maintained in the population for many generations (Papaj 1994). Historical contingencies, such as climate change during the Holocene, that might have affected conditions allowing coexistence of bighorn sheep and mountain lions or allow gene flow between the Eagle Mountain population and populations in areas inhabited by lions, could mean there has been inadequate time for evolution in response to absence of predators, resulting in the observed partially adaptive response. Insufficient additive genetic variation for vigilance could also prevent the Eagle Mountain population from responding to selection (Falconer 1989). For example, low heritability has been found to be a cause for partial response to relaxed selection in antipredator behavior of ground squirrels (Coss 1999). Additionally, phylogenetic constraints may prevent adaptive change in the physiological set points of the control of vigilance and the degree that individual vigilance is influenced by external cues and learning.

The non-optimal and apparently nonadaptive mean norm of reaction for vigilance behavior and persistence of high mean vigilance in the Muddy Mountain population suggests there may be little or no cost to vigilance for sheep in this population. Both selection and heritability are required for evolution of vigilance. Variance in the intensity of natural selection to lower the amount of time individuals spend in vigilance, and thus increase the amount of time spent foraging, could contribute to the nonadaptive pattern of
vigilance among sheep populations in low-elevation mountain ranges. Vegetation growth in the Mojave Desert is highly dependent on the amount of available precipitation (Beatley 1974). Substantial variation in rainfall, characteristic of desert environments, occurs annually, seasonally, and geographically (Smith et al. 1997). This variation could cause differences in forage quality and availability between mountain ranges (Warrick and Krausman 1987; Bleich et al. 1997), which could, in turn, affect the intensity of selection to increase foraging efficiency (and decrease vigilance) in response to relaxed predation. Differences in forage variety and abundance between mountain ranges have attributed to differences in foraging efficiency between ewes in two populations in the Sonoran Desert (Warrick and Krausman 1987). Without selection for a decrease of vigilance, mean vigilance could persist at a high level as a learned response that had been retained through many generations. Behavioral traits may be nonadaptive if they are the result of cultural learning rather than being genetically programmed (Reichert 1999). Learned responses may be maintained in populations for many generations (Curio et al. 1978a, b; Knight 1984; Conover 1987; Thornhill 1989; Maloney and McLean 1995). Underwood (1982) suggested that even when the likelihood of predation is low, vigilance in ungulates nonetheless appears to be affected by the possibility of predation. In his study of vigilance in African ungulates, where predation risk was low, animals still adjusted vigilance with respect to environmental factors and perceived predation risk. Kavaliers and Choleris (2001) suggest that animals may overestimate the risk of predation to avoid the relatively high cost of underestimation.

Parallel directional selection on a correlated character with an adaptive function could also constrain evolution of vigilance behavior and cause random or nonadaptive norms of
reaction. Correlation of behavioral traits related to survivorship during years of high lion predation has been shown to occur in bighorn sheep (Real and Festa-Bianchet 2003). Selection on correlated characters could have constrained adaptive adjustment of vigilance behavior in bighorn sheep populations under both predation regimes. Correlated responses may be maintained through linkage disequilibria or pleiotropic effects of the same genes (Price and Langen 1992). If vigilance is correlated with another trait with an adaptive function, optimal levels of vigilance might not evolve as predicted. Results of a comparison of ewe survival during years of high and low mountain lion predation indicated that predation was age-specific and responsible for covariance between temperament and survival (Real and Festa-Bianchet 2003). Direct selection favored bold ewes during periods of predation by mountain lions. There was no selection on boldness during years without predation. Additionally, results of a study by Reale et al. (2000) found that age at primiparity (first birth) had a negative phenotypic correlation with docility and boldness, where bold ewes had higher weaning success than shy ewes.

Conclusions
The results presented in this chapter show that the lack of fit for predicted patterns of vigilance between populations of bighorn sheep in habitat with resident mountain lions versus habitat without resident lions is at least partially due to high variance of vigilance among the three replicate populations of bighorn sheep in habitat without resident lions. This variance was attributed to the persistence of high mean vigilance levels, despite the potential for relaxed selection, in the Muddy and Eagle Mountain populations, and a non-optimal and nonadaptive plastic response of vigilance to group size and terrain type in the
Muddy Mountains population. Vigilance behavior in the River Mountain population matched the predicted patterns of an adaptive response to relaxed selection, as did the flat norms of reaction for vigilance expressed across group size and terrain type in the Eagle Mountains.

In Chapter 4, I compare changes in vigilance in populations of sheep translocated at different intervals of time from the River Mountains into habitat occupied by mountain lions to determine whether populations under relaxed predation pressure retain sufficient adaptive plasticity to adjust vigilance behavior in response to increased predation risk, and whether variance in adaptive responses between these populations also contributed to the lack of geographic variation of vigilance observed in Chapter 2.

Literature Cited


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Curio, E.1975. The functional organization of anti-predator behavior in the pied


CHAPTER 4

VIGILANCE BEHAVIOR IN TRANSLOCATED POPULATIONS OF DESERT BIGHORN SHEEP (*OVIS CANADENSIS NELSONI*): RESPONSE TO INCREASED PREDATION RISK

Abstract

Efforts to restore extirpated bighorn sheep populations in the western U.S. have relied greatly on translocation programs. In Nevada, most of the desert-dwelling sheep used as founder stock are taken from the River Mountains in Lake Mead National Recreation Area. The River Mountains are a low-elevation mountain range in the Mojave Desert, and are uninhabited by resident mountain lions. Norms of reaction for vigilance expressed across group size and terrain type within the River Mountains resemble predicted patterns of a population under relaxed selection. I compared changes in vigilance in populations of bighorn sheep translocated at different intervals of time from the River Mountains into habitat occupied by mountain lions to determine whether populations under relaxed predation pressure retain sufficient adaptive plasticity to adjust vigilance behavior in response to increased predation risk, and whether variance in adaptive responses among translocated populations contributed to the lack of fit to predicted patterns of optimal or adaptive vigilance observed in Chapter 2. In the Delamar Range (Nevada), behavioral adjustments took place within two years after sheep were released with increased vigilance observed under conditions of highest perceived
predation risk. Small groups of sheep foraging away from escape terrain had higher adjusted mean vigilance in the Delamar Range (25.5%) than in the River Mountains (17.3%). The greatest change in vigilance occurred in the oldest translocation population. Bighorn ewes in Zion N.P. (Utah) responded to increased predation risk with a significant increase in overall mean vigilance (30.0%) and plastic adjustments in vigilance behavior relative to group size that match optimal or adaptive predictions. Mean vigilance of bighorn ewes foraging in small and medium groups was greater than large groups on escape terrain and away from escape terrain.

Sheep from the Pancake Range (Nevada) retained mean norms of reaction for vigilance that were similar to the River Mountains population. Although mean vigilance of ewes foraging away from escape terrain in the three selected group sizes was higher in the Pancake Range than in the River Mountains, the difference was not significant for small groups, which have the highest perceived predation risk. Results from this and the previous chapter (Chapter 3) indicate that high variability in vigilance among the three replicate populations of native desert bighorn sheep with relaxed selection, combined with the nonadaptive response of ewes in the Pancake Range, contributed to the large-scale pattern of non-optimal or nonadaptive variation in vigilance observed in Chapter 2. Given that some of the populations do match prediction of optimal or adaptive norms of reaction for vigilance behavior, it appears that there are a variety of processes and contingencies that combine to generate the observed variability in behavior of bighorn sheep.
Introduction

Translocation of animals is a widely used conservation tool to re-establish extirpated populations or to augment critically small populations (World Conservation Union 1993). Although translocations can be very effective, only an estimated 50% are considered to be successful (Griffith et al. 1989; Wolf et al. 1996; Ramey et al. 2000). Successful reintroductions of ungulate populations in North America include American bison (*Bison bison*), elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*).

In North America, the distribution and abundance of bighorn sheep have declined from greater than 500,000 in the early 1800's (Valdez 1988) to an estimated 185,000 animals in the 1990's (Krausman 2000). Population declines have been attributed to diseases transmitted from domestic livestock, unregulated hunting, and habitat loss or deterioration (McQuivey 1978). Efforts to restore extirpated sheep populations have relied greatly on translocation programs and, as a result, over 50% of all present day populations have originated from translocations (Bailey 1990; Jessup et al. 1995). Despite these successes, most restoration attempts have not been successful (Risenhoover 1988). As an example, only 41 of 100 translocations that took place in six western states from 1923 to 1997 were considered successful (Singer et al. 2000).

When searching for causes of failure of sheep translocations, researchers have examined the effects of disease, predation, and genetic bottlenecks (Ramey et al. 2000), but have not examined the role of behavior and its effect on the success of reintroductions. Behavior can vary significantly between source and reintroduction populations (Zwank et al. 1988), particularly when there are differences in habitat or...
predation risk between source and translocated populations. Learning may play an important role in the success of reintroduced populations and could cause much of the behavioral divergence that may be observed between source and translocated populations.

In this study, I examine changes in vigilance in populations of bighorn sheep translocated at different intervals of time from the River Mountains into habitat occupied by mountain lions to determine whether the River Mountain population, under relaxed predation pressure, retains sufficient adaptive plasticity to adjust vigilance behavior in response to increased predation risk. In addition, I determined whether potential variance in optimal or adaptive responses among translocated populations contributed to the lack of fit to predicted patterns of optimal vigilance observed in Chapter 2.

Adaptive phenotypic responses to the environment (phenotypic plasticity) are thought to be able to evolve in populations with predictable environmental heterogeneity (Via and Lande 1985; Scheiner 1993; Via et al. 1995). Depending upon the level of genetic variation for phenotypic plasticity, adaptive plasticity in vigilance behavior could evolve in response to natural selection of different phenotypic values in environments with different risk of predation. If trait frequencies of reaction norms for vigilance are the result of selection acting on a correlated trait, or non-selective forces such as genetic drift, or recent changes in the environment, behavioral divergence among populations with and without mountain lions could be non-adaptive or random (Endler 1986; Reeve and Sherman 1993).

As of 1994, 971 bighorn sheep in Nevada have been translocated into 24 formerly occupied mountain ranges (Cummings and Stevenson 1995). A majority of desert-
dwelling sheep used as founder stock is taken from the River Mountains in the Lake Mead National Recreation Area, Nevada. The River Mountains are a typical low elevation Mojave Desert range characterized by desert scrub and desert wash plant communities (Leslie and Douglas 1979). Populations in low-elevation mountain ranges (< 1,000 m) in the Mojave Desert have inhabited a relatively stable environment since the end of the last glacial age; vegetation has consisted of desert scrub communities for approximately 8,000 to 10,000 years (Spaulding 1990). Historic predator pressure on these populations is unknown, but mountain lions are generally not present in low-elevation mountain ranges that are uninhabited by deer (Berger and Wehausen 1991).

Habitat at relocation sites may or may not be similar to that of the River Mountains. A number of these animals have been transplanted into mountain ranges with substantial areas of pinyon-juniper woodland and ponderosa pine forest. Examples of such areas are the Hot Creek, Toquima, Pancake, and East Mountain Ranges in the Great Basin, Nevada, and Zion National Park (N.P.), Utah (McCutchen 1979). Many of these translocation sites are also occupied by mountain lions (Ashman et al. 1983). Mountain lion predation has had deleterious effects on the success of sheep restoration programs. When 22 bighorn sheep from the River Mountains were released into Zion N. P., mountain lions killed 20% within the first 6 months (McCutchen 1979), and in the Wassuk and Snake Ranges of northern Nevada, bighorn sheep introductions failed because of lion predation (Berger and Wehausen 1991). In the River Mountains, mountain lions rarely have been sighted and these sighted lions were migrants, not residents (Leslie and Douglas 1979).
Hypotheses for a Behavioral Response to Translocation

How transplanted mountain sheep respond to differences in habitat and increased predation can be determined by characteristics of the trait for vigilance. Translocated populations may exhibit adaptive plastic changes in vigilance that covary with ecological variables (terrain type and group size) to yield an "optimal" response for the new habitat that could be expressed immediately by most or all individuals, perhaps in response to habitat cues. Adaptive behavioral responses of vigilance behavior in translocated sheep populations could also increase over time due to cultural or maternal learning in response to predator encounters or due to evolution of vigilance plasticity such that the increase in vigilance would be positively correlated with duration of exposure to predators.

In this chapter, I examine vigilance behavior in sheep translocated from the River Mountains into habitat with resident mountain lions to determine whether populations under relaxed predation pressure have the ability to adjust vigilance behavior in response to increased predation risk. I assumed individual vigilance was a plastic trait and tested for population divergence in norms of reaction expressed across group size and terrain between the source population (a low-elevation mountain range without resident mountain lions) and three translocated populations of bighorn sheep. All three translocation sites were inhabited by mountain lions, but the translocations occurred two, ten, and twenty-two years ago.

Predictions for an optimal or adaptive plastic behavioral response to increased predation risk in translocated sheep populations were as follows: (1) there will be an immediate response to increased perception of predation risk; mean vigilance and mean norms of reaction for vigilance expressed across environmental covariates of translocated
populations will diverge from the source population and will be similar for all translocated populations; or (2) translocated populations will show immediate partial divergence of mean vigilance and mean norms of reaction for vigilance expressed across environmental covariates followed by a pattern of increasing divergence in overall mean vigilance and mean reaction norms through time (i.e. with increasing age of translocation population). The null hypothesis was that there is no difference in natural selection of vigilance behavior and no divergence of mean vigilance between the source and translocated populations. An alternative hypothesis was that there is random divergence among populations due to genetic drift, or a correlated response to selection of unknown traits.

The expected plastic adjustments of vigilance to ecological variables consistent with adaptive plasticity were: (1) vigilance will decrease with increasing group size, but the magnitude of this response will be determined by distance from escape terrain (i.e., steep, rocky slopes); and (2) vigilance will increase with increased distance from escape terrain, but the magnitude of the response will be determined by group size.

Methods and Analysis

**Study Sites**

Vigilance behavior was sampled from desert bighorn sheep inhabiting the River Mountains, Nevada, the source population, and three populations translocated into the Delamar and Pancake Ranges in Nevada, and Zion National Park, Utah (Figure 1, Chapter 2). The River Mountains are a low-elevation mountain range in the Mojave Desert uninhabited by resident mountain lions; translocation sites, are located within the
Great Basin and the Colorado Plateau, are inhabited by lions (Table 10). Smaller predators, such as coyotes and golden eagles, were also present in all mountain ranges.

The exact number of founder animals killed by lions in the Delamar and Pancake Range populations is unknown; after their release, these animals were not studied as intensively as the population in Zion N.P. (see McCutchen 1979), but Nevada Division of Wildlife personnel documented predation by mountain lions on at least one of twelve sheep equipped with radio-telemetry collars during the first two years following translocation. Sample size of data collected for the Delamar Range population was less than for the other three populations because I discontinued data collection when additional bighorn sheep were released into the mountain range in 2000. Nevada Division of Wildlife has reported evidence of lion kills in the Pancake Range, but the intensity of mountain lion predation on these sheep is unknown (Pat Cummings, pers. comm. 2003). During this study lion tracks were observed in sheep habitat, but no physical evidence of predation was observed.

Within the first six months after sheep were released into Zion National Park, 20% of the founder animals were killed by mountain lions (McCutchen 1979). By 1980, only half of the founder population was known to be alive, and by the mid 1980’s so few animals were seen that the translocation was presumed a failure due to predation and disease. In the 1990’s park personnel and visitors began reporting groups of sheep, and results of a demographic study showed the population had increased to an estimated 67 animals despite continuing predation by lions (McCutchen et al. 1994). During this study, lion tracks were often observed in sheep habitat, and one of twelve radio-collared ewes was killed by a mountain lion.
Table 10. Translocated and source desert bighorn sheep populations used in the study. Transplant populations were reintroduced into historic sheep habitat that was uninhabited by bighorn sheep at the time of the reintroductions. Bighorn sheep translocated into the Pancake Range were not monitored closely after release. Although the Nevada Division of Wildlife has received a number of reports of sheep killed by lions in the Pancake Range, the exact number of confirmed deaths is unknown.

<table>
<thead>
<tr>
<th>Mountain Range (Population)</th>
<th>Geographic Location</th>
<th>Transplant History (Translocation Year)</th>
<th>Confirmed Deaths Due to Mountain Lion Predation Within Two Years of Release</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat Without Resident Mountain Lions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>River Mountains Mojave Desert Native population Source for transplants</td>
<td>N/A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat With Resident Mountain Lions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zion National Park Colorado Plateau 30 Sheep (1977 and 1979)</td>
<td>5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*A lion killed one of 5 ewes fitted with radio telemetry collars during the study.
**Mountain lion tracks were observed in areas occupied by sheep during the study.
Behavioral data were collected from bighorn sheep in the River Mountains during 1987 and 1988. Data were collected from the other five populations from 1995 through 2000. Vigilance levels were quantified as the proportion of time during a foraging bout that an animal stopped feeding to raise its head above the shoulders and look around at the surrounding terrain. Vigilance behavior of bighorn sheep was observed and recorded using a combination of focal animal and scan sampling techniques (Altmann 1974). To eliminate variance associated with differences between ewe and ram behavior, data were collected from ewes only. Ewes were also selected because they are subject a higher proportion of deaths due to predation than are rams (Berger 1991). Records were made of location, distance from the base of the nearest cliffs or steep, rocky slopes (termed “escape terrain”), vegetation type within 2 meters, group size, and species composition. Visibility, or the amount of visual obstruction due to vegetation, was not included in the analysis because in the Delamar Range bighorn sheep were only found in areas with low vegetation growth and thus high visibility.

Once a group of sheep were located and > 60% of the animals were feeding, a focal animal was randomly selected and observed continuously for 5 minutes (300 sec). Sheep were observed with a Celestron C-5 telescope (90 power) and could be easily seen from ca. 1 km. Data were only collected on animals that were unaware of my presence and I made an effort to collect data from a location as far from the animals as possible. If animals were observed looking directly towards me in a non-random fashion, data collection stopped. All behavioral activities were recorded continuously into a tape recorder. A focal animal was defined as vigilant when it lifted its head to shoulder height.
and surveyed its surroundings. Following the focal animal sample, another ewe was randomly chosen, excluding the previous animal, until all members of the group had been observed. No attempt was made to discriminate between ‘active’ versus ‘weak’ vigilance (Alados, 1985), to determine whether vigilance was directed at specific objects (see LaGory, 1986), or whether sheep were engaged in decision-making concerning moving to other foraging patches (e.g., in buffalo; Prins 1996). Instead, I assumed that ewes were using the head-up posture to gather information on all possible factors. Behavioral data were transcribed using a stopwatch to measure scan durations to the nearest second and enable calculation of the proportion of time spent vigilant. Data was only collected on animals that were unaware of my presence and I made an effort to collect data from as far from the animals as possible. Observations were only made on sheep that did not show signs that they had observed me. If animals were observed looking directly towards me in a non-random fashion, I did not collect behavioral data because I was interested in the overall, or general vigilance maintained in each population and not the response of ewes to a human observer. In addition, it is also possible that, depending on their degree of acclimation to humans, a population of sheep may react less alarmingly to a human observer than to a potential predator.

Statistical Analysis

To test the hypotheses of an adaptive phenotypic response in vigilance behavior in translocated populations, comparisons of mean vigilance between bighorn sheep populations were performed using analysis of covariance following the technique described in Littell et al. (2001) and discussed in detail in Chapter Two. Bighorn sheep population and relation to escape terrain ("on or <100 m from cliffs or steep, rocky slopes
versus >100 m from cliffs or steep, rocky slopes) were considered main effects and group size was treated as a covariate. Categories for distance from escape terrain were based upon Berger (1991). Prior to the analysis, vigilance was arcsine transformed to meet assumptions of normality and homogeneity of variance (Zar 1999). The assumption of homogeneous variance was evaluated with a plot of the residuals versus the estimated treatment means. Residuals were examined to verify normality and used to provide visual evaluations of the analysis of variance assumptions for homogeneous variances and normal distribution of experimental errors.

Results

Total mean vigilance of ewes in the River Mountains population (translocation source) was 9.9 ± 0.7% (S.E.), with a range of 0 to 51.0% (n = 133). Total mean vigilance of the translocated populations from earliest to latest translocation was 17.7 ± 1.2% for Zion N.P. (range 0 to 60.3%; n = 118), 13.9 ± 1.3% for the Pancake Range (range 0 to 61.3%; n = 82), and 11.6 ± 1.5% for the Delamar Range (range 0 to 36.0%; n = 42) (Figure 8).

Average adult group size in the River Mountains was 8 (median = 6), with a range of 2 to 30 sheep (n = 81). In the Delamar Range, mean group size was 7 (median = 9), and ranged from 4 to 10 animals (n = 6). Group size was largest in the Pancake Range, where the mean was 14 (median = 9) and ranged from 2 to 40 animals (n = 25). Average adult group size was 7 in Zion N.P. (median = 7; range = 2 to 11; n = 17). The Kruskal-Wallis Test (Zar 1999) was used to compare median group size between the four populations because group size data were non-normal even after log transformation. Median group
Figure 8. Population means for the percentage of time desert bighorn ewes are vigilant during foraging bouts. The River Mountains population inhabits a low-elevation mountain range without resident mountain lions. Bighorn sheep in the Delamar Range, Pancake Range and Zion N. P. were originally translocated from the River Mountains and are in habitat with resident mountain lions. Vertical bars are standard errors.
size of sheep from the Pancake Range was significantly higher than that of the River Mountains and Zion N.P. populations ($H_{0.05, 81, 625, 17} = 8.325; P = 0.040$).

**Determining the Form of the Covariate in the Model**

Results of the slopes-equal-to-zero model showed a significant group-size-by-population-by-escape-terrain interaction ($F_{8, 359} = 2.22; P = 0.026$), indicating that not all slopes and intercepts are equal to zero and that group size should be included as a covariate in the model. The equal slopes hypothesis was also rejected due to a significant group-size-by-population interaction ($F_{3, 362} = 2.66, P = 0.048$), signifying that the relationship between group size and vigilance was not the same across all populations.

Figure 9 shows regressions of group size on percent vigilance for the source and translocated populations across all terrain types. The slope of the regression was not different from zero for the River Mountains and Pancake Range populations (Table 11). Slope of the regression for ewes in the Delamar Range was significantly different from zero and in Zion N.P. the slope differed at $P = 0.059$ (Table 11). Accordingly, a multiple comparison procedure on the slopes was performed using the unequal slopes model.

Mean vigilance was compared at low (4), medium (9), and high (14) group sizes. These values were chosen to include a range of group sizes that would fit all populations in the analysis.

**Divergence of Vigilance**

To test the adaptive hypothesis of an adaptive response in vigilance behavior in translocated populations as a result of increased predation risk, multiple contrasts were used to examine the main effect of populations (source versus translocated) across terrain types (escape terrain versus non-escape terrain) at the three group size values. Results of
Figure 9. Linear regressions showing the relationship between group size and vigilance of desert bighorn ewes belonging to the River Mountains, a low-elevation mountain range without resident mountain lions, and three populations originally translocated from the River Mountains to habitat with resident mountain lions.
Table 11. Regression statistics for group size (across all terrain types) and proportion of time spent vigilant during foraging bouts of bighorn sheep populations translocated from the River Mountains to habitat with resident mountain lions.

<table>
<thead>
<tr>
<th>Population</th>
<th>Regression Coefficient</th>
<th>Standard Error</th>
<th>t Statistic</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>River Mountains</td>
<td>-0.044</td>
<td>±0.039</td>
<td>-0.162</td>
<td>0.263</td>
</tr>
<tr>
<td>Delamar Range</td>
<td>-1.725</td>
<td>±0.655</td>
<td>-2.635</td>
<td>0.012</td>
</tr>
<tr>
<td>Pancake Mountains</td>
<td>-0.052</td>
<td>±0.081</td>
<td>-0.640</td>
<td>0.524</td>
</tr>
<tr>
<td>Zion National Park</td>
<td>-0.604</td>
<td>±0.317</td>
<td>-1.906</td>
<td>0.059</td>
</tr>
</tbody>
</table>

The contrasts showed divergence in mean vigilance between the source population and foraging in Zion N. P (oldest transplant) and the Delamar Range (youngest transplant) was greater across all terrain types than adjusted mean vigilance of sheep in the River Mountains (P = 0.056 and P = 0.026, respectively). At medium and large group sizes, adjusted mean vigilance across all terrain types was similar (Table 12). The increased vigilance of small groups (i.e., group size under highest predation risk) in the Delamar Range and Zion National Park is consistent with hypotheses of an adaptive behavioral response over time to lion predation as the result of learned behavior, or to evolution of a two of the translocated populations. Adjusted mean vigilance for small groups of sheep heightened plastic response to predator encounters (heightened ability to learn). Behavior patterns of sheep in the Pancake Range (lack of divergence from the River Mountains population) were inconsistent with those expected under adaptive hypotheses.

Norms of Reaction for Vigilance Expressed Across Group Size and Terrain

Multiple comparisons were then used to compare vigilance in relation to escape terrain for each mountain range (population) at the three group size values (Table 13).
Table 12. Results of the comparison of main effects for mean vigilance across all terrain types between bighorn ewes in habitat without resident mountain lions (source population) and three populations translocated into habitat with resident mountain lions. Adjusted mean vigilance was compared at three group size values from each of the different regression models. Degrees of freedom were determined using the Satterwaite approximation.

<table>
<thead>
<tr>
<th>Contrasts for Main Effects (Populations)</th>
<th>Covariate value (Group size)</th>
<th>Adjusted Mean (± SE)</th>
<th>Adjusted Mean (± SE)</th>
<th>t Value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>River Mtns vs. Delamar Range</td>
<td>4</td>
<td>16.1 (±1.5)</td>
<td>23.5 (±3.6)</td>
<td>-2.23</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>16.7 (±1.5)</td>
<td>16.5 (±2.3)</td>
<td>0.10</td>
<td>0.919</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>17.3 (±2.4)</td>
<td>9.5 (±5.2)</td>
<td>1.57</td>
<td>0.117</td>
</tr>
<tr>
<td>River Mtns vs. Pancake Range</td>
<td>4</td>
<td>16.1 (±1.5)</td>
<td>21.3 (±2.7)</td>
<td>0.26</td>
<td>0.794</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>16.7 (±1.5)</td>
<td>21.9 (±2.3)</td>
<td>1.23</td>
<td>0.219</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>17.3 (±2.4)</td>
<td>22.6 (±2.5)</td>
<td>1.54</td>
<td>0.124</td>
</tr>
<tr>
<td>River Mtns vs. Zion N.P.</td>
<td>4</td>
<td>16.1 (±1.5)</td>
<td>27.6 (±2.3)</td>
<td>-1.91</td>
<td>0.056</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>16.7 (±1.5)</td>
<td>23.5 (±1.8)</td>
<td>-0.20</td>
<td>0.839</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>17.3 (±2.4)</td>
<td>19.5 (±2.9)</td>
<td>0.56</td>
<td>0.574</td>
</tr>
</tbody>
</table>
Results showed no significant adjustment of mean vigilance in relation to escape terrain at any of the three selected group sizes for any population (Figure 10). Norms of reaction for vigilance expressed across group size and relation to escape terrain of all three translocated populations were similar to the River Mountains population, where the norm of reaction for vigilance expressed across group size and escape terrain matched predictions of a response to relaxed selection from high predation risk. Results of the pairwise comparisons of terrain type (escape terrain versus non-escape terrain) between translocated and source populations at group sizes 4, 9 and 14 showed evidence of divergence from the River Mountains ewes for two of the translocated populations (Figure 11). In the Delamar Range, adjusted mean vigilance of bighorn sheep in small groups foraging further than 100 meters from escape terrain was significantly greater than that of small groups foraging under similar conditions in the River Mountains (p = 0.014). There was no divergence among these populations when ewes foraged away from escape terrain in medium- and large-sized groups (Table 14).

In Zion N.P., ewes feeding away from escape terrain in small- and medium-sized groups had higher levels of vigilance than ewes foraging under similar conditions in the River Mountains (p = 0.000 and 0.002 for small and medium groups, respectively). This behavior is consistent with predicted adaptive responses to increased predation risk.

In the Pancake Range, however, norms of reaction for vigilance did not appear to fit an adaptive pattern. Whereas mean vigilance was higher in the Pancake Range than in the River Mountains, the difference was only significant for medium (p = 0.023) and large group sizes (p = 0.016), and not for small groups where perceived risk is considered to be higher. When foraging on escape terrain, adjusted mean vigilance of ewes in the
Table 13. Results of the comparisons between terrain types for adjusted mean vigilance of bighorn ewes from the source and translocated populations. Terrain types were areas on or less than 100 meters from the nearest cliffs or steep, rocky slopes (escape terrain) and areas greater than 100 meters from the nearest cliffs or steep, rocky slopes (non-escape terrain). Adjusted mean vigilance was compared at three group size values from each of the different regression models. Degrees of freedom were determined using the Satterwaite approximation.

<table>
<thead>
<tr>
<th>Contrasts for Main Effects (Population)</th>
<th>Covariate value (Group size)</th>
<th>Escape terrain Adjusted Mean (± SE)</th>
<th>Non-Escape Terrain Adjusted Mean (± SE)</th>
<th>P Value (df =362)</th>
</tr>
</thead>
<tbody>
<tr>
<td>River Mountains</td>
<td>4</td>
<td>15.2 (±1.9)</td>
<td>17.1 (±1.4)</td>
<td>0.353</td>
</tr>
<tr>
<td>River Mountains</td>
<td>9</td>
<td>16.9 (±0.1)</td>
<td>16.6 (±2.2)</td>
<td>0.918</td>
</tr>
<tr>
<td>River Mountains</td>
<td>14</td>
<td>18.1 (±3.7)</td>
<td>16.6 (±1.1)</td>
<td>0.692</td>
</tr>
<tr>
<td>Delamar Range</td>
<td>4</td>
<td>21.6 (±4.1)</td>
<td>25.5 (±3.2)</td>
<td>0.280</td>
</tr>
<tr>
<td>Delamar Range</td>
<td>9</td>
<td>15.5 (±1.9)</td>
<td>17.59 (±2.7)</td>
<td>0.500</td>
</tr>
<tr>
<td>Delamar Range</td>
<td>14</td>
<td>9.3 (±4.8)</td>
<td>9.7 (±5.6)</td>
<td>0.917</td>
</tr>
<tr>
<td>Pancake Range</td>
<td>4</td>
<td>21.8 (±3.9)</td>
<td>20.7 (±1.6)</td>
<td>0.798</td>
</tr>
<tr>
<td>Pancake Range</td>
<td>9</td>
<td>23.3 (±3.3)</td>
<td>20.5 (±1.3)</td>
<td>0.429</td>
</tr>
<tr>
<td>Pancake Range</td>
<td>14</td>
<td>24.9 (±3.8)</td>
<td>20.3 (±1.1)</td>
<td>0.257</td>
</tr>
<tr>
<td>Zion National Park</td>
<td>4</td>
<td>25.2 (±1.3)</td>
<td>30.0 (±3.3)</td>
<td>0.137</td>
</tr>
<tr>
<td>Zion National Park</td>
<td>9</td>
<td>22.0 (±1.1)</td>
<td>25.1 (±2.5)</td>
<td>0.252</td>
</tr>
<tr>
<td>Zion National Park</td>
<td>14</td>
<td>18.8 (±2.3)</td>
<td>20.2 (±3.5)</td>
<td>0.700</td>
</tr>
</tbody>
</table>
Figure 10. Mean norms of reaction for vigilance in relation to group size and escape terrain for three translocated populations of desert bighorn ewes and their source population. The source population inhabits the River Mountains, an area without resident lions. Translocated populations are in habitat with resident mountain lions. Terrain types were areas on or less than 100 meters from cliffs or steep, rocky slopes (escape terrain) and areas greater than 100 meters from cliffs or steep, rocky slopes (non-escape terrain). Lines connecting means are not regression lines. Vertical lines are standard error bars. See Table 13 for significant differences among adjusted means.
Figure 11. Comparison of mean norms of reaction for vigilance expressed across group size and location in relation to escape terrain for three translocated populations of desert bighorn ewes and their source population. The source population inhabits the River Mountains, an area without resident lions. The translocated populations inhabit areas with resident mountain lions. Terrain types were areas on or < 100 meters from cliffs or steep, rocky slopes (escape terrain) and areas > 100 meters from cliffs or steep, rocky slopes (non-escape terrain). Lines connecting means are not regression lines. Vertical lines are standard error bars.
Non-Escape Terrain

Adjusted Vigilance

Group Size

River Mountains
Delamar Range
Pancake Range
Zion National Park

Escape Terrain

Adjusted Vigilance

Group Size

River Mountains
Delamar Range
Pancake Range
Zion National Park

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Table 14. Results of multiple comparisons for percent mean vigilance between source (River Mountains) and translocated populations of bighorn sheep ewes foraging away from escape terrain (> 100 m from cliffs or steep, rocky slopes). Adjusted mean vigilance was compared at three group size values from each of the different regression models. Degrees of freedom were determined using the Satterwaite approximation.

<table>
<thead>
<tr>
<th>Contrasts for Main Effects (Populations)</th>
<th>Covariate value (Group size)</th>
<th>Adjusted Mean (± SE) River Mtns</th>
<th>Adjusted Mean (± SE) Delamar Range</th>
<th>t Value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Away from Escape Terrain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>River Mtns vs. Delamar Range</td>
<td>4</td>
<td>17.3 (±1.1)</td>
<td>25.5 (±3.2)</td>
<td>-2.47</td>
<td>0.014</td>
</tr>
<tr>
<td>River Mtns vs. Delamar Range</td>
<td>9</td>
<td>16.8 (±0.9)</td>
<td>17.6 (±2.7)</td>
<td>-0.26</td>
<td>0.796</td>
</tr>
<tr>
<td>River Mtns vs. Delamar Range</td>
<td>14</td>
<td>16.6 (±1.1)</td>
<td>9.7 (±5.6)</td>
<td>1.21</td>
<td>0.229</td>
</tr>
<tr>
<td>River Mtns vs. Pancake Range</td>
<td>4</td>
<td>17.3 (±1.1)</td>
<td>20.7 (±1.6)</td>
<td>-1.82</td>
<td>0.069</td>
</tr>
<tr>
<td>River Mtns vs. Pancake Range</td>
<td>9</td>
<td>16.8 (±0.9)</td>
<td>20.5 (±1.3)</td>
<td>-2.28</td>
<td>0.023</td>
</tr>
<tr>
<td>River Mtns vs. Pancake Range</td>
<td>14</td>
<td>16.6 (±1.1)</td>
<td>20.3 (±1.1)</td>
<td>-2.42</td>
<td>0.016</td>
</tr>
<tr>
<td>River Mtns vs. Zion N.P.</td>
<td>4</td>
<td>17.3 (±1.1)</td>
<td>30.0 (±3.3)</td>
<td>-3.71</td>
<td>0.000</td>
</tr>
<tr>
<td>River Mtns vs. Zion N.P.</td>
<td>9</td>
<td>16.8 (±0.9)</td>
<td>25.1 (±2.5)</td>
<td>-3.13</td>
<td>0.002</td>
</tr>
<tr>
<td>River Mtns vs. Zion N.P.</td>
<td>14</td>
<td>16.6 (±1.1)</td>
<td>20.2 (±3.5)</td>
<td>-0.99</td>
<td>0.322</td>
</tr>
</tbody>
</table>

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Delamar and Pancake Ranges did not diverge from the River Mountains at any of the three group sizes (Table 15). In Zion N.P., sheep in both small ($p = 0.000$) and medium groups ($p = 0.023$) were more vigilant than sheep in the River Mountains population.

Discussion

In this chapter, I examine vigilance behavior of bighorn sheep ewes belonging to populations translocated from the River Mountains, Nevada, which have no resident mountain lions, into habitat with resident mountain lions. Specifically, I wished to determine whether populations under relaxed predation pressure retain adequate adaptive plasticity to adjust vigilance behavior in response to increased predation risk, and if observed variance in adaptive responses among these populations contributed to the lack of fit to predicted patterns of optimal or adaptive vigilance observed in Chapter 2.

Vigilance of Ewes in the Delamar Range

Bighorn sheep in the River Mountains, lacking large predators, do not adjust vigilance in response to differences in group size or in relation to escape terrain (Chapter 3). However, when sheep from this population were translocated to the Delamar Range, they responded with a plastic adjustment in vigilance under conditions of highest perceived predation risk. Within two years translocated bighorn ewes (founder individuals) in the Delamar Range responded to predator-occupied environments with an overall increase in mean vigilance when foraging in small groups (averaged across terrain type).

The increase in vigilance at small group sizes could be attributed to an interactive effect between terrain and group size. Small groups of bighorn ewes foraging in areas
Table 15. Results of the multiple comparisons for percent mean vigilance between source (River Mountains) and translocated populations of bighorn sheep ewes foraging on or near escape terrain (<100 m). Adjusted mean vigilance was compared at three group size values from each of the different regression models. Degrees of freedom were determined using the Satterwaite approximation.

<table>
<thead>
<tr>
<th>Contrasts for Main Effects (Populations)</th>
<th>Covariate value (Group size)</th>
<th>Adjusted Mean (± SE) River Mtns</th>
<th>Adjusted Mean (± SE) Delamar Range</th>
<th>t Value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>On or Near Escape Terrain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>River Mtns vs. Delamar Range</td>
<td>4</td>
<td>15.15 (±1.8)</td>
<td>21.6 (±4.1)</td>
<td>1.52</td>
<td>0.131</td>
</tr>
<tr>
<td>River Mtns vs. Delamar Range</td>
<td>9</td>
<td>16.6 (±2.2)</td>
<td>23.3 (±3.3)</td>
<td>0.42</td>
<td>0.678</td>
</tr>
<tr>
<td>River Mtns vs. Delamar Range</td>
<td>14</td>
<td>18.1 (±3.7)</td>
<td>24.9 (±3.8)</td>
<td>1.76</td>
<td>0.079</td>
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<tr>
<td>River Mtns vs. Pancake Range</td>
<td>4</td>
<td>15.15 (±1.8)</td>
<td>21.6 (±4.1)</td>
<td>1.68</td>
<td>0.094</td>
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<td>23.3 (±3.3)</td>
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<td>River Mtns vs. Pancake Range</td>
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<td>24.9 (±3.8)</td>
<td>1.68</td>
<td>0.093</td>
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<tr>
<td>River Mtns vs Zion N.P.</td>
<td>4</td>
<td>15.15 (±1.8)</td>
<td>25.2 (±1.3)</td>
<td>4.48</td>
<td>0.000</td>
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<tr>
<td>River Mtns vs Zion N.P.</td>
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<td>16.6 (±2.2)</td>
<td>22.0 (±1.1)</td>
<td>2.28</td>
<td>0.023</td>
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<tr>
<td>River Mtns vs Zion N.P.</td>
<td>14</td>
<td>18.1 (±3.7)</td>
<td>18.8 (±2.3)</td>
<td>0.85</td>
<td>0.854</td>
</tr>
</tbody>
</table>
away from escape terrain in the Delamar Range were more vigilant than ewes foraging under similar circumstances in the River Mountains. Mean vigilance of large and medium groups was similar to that of the River Mountains. Ewes in small groups could be expected to increase vigilance first because it is widely assumed that animals in small group sizes are under higher predation risk than those in larger groups (Elgar 1989; Lima and Dill 1990).

Because of the potentially complex plastic adjustments of vigilance in response to local environmental variables, differences between source and translocated populations may reflect learned behavioral differences in vigilance for populations that are genetically similar. Where large predators have been recently extirpated (less than 150 years), ungulate populations have been observed to respond immediately to reintroduction of predators by increasing predation detection behavior (Hunter and Skinner 1998; Berger 2001). In an area in South Africa where historical predators had been absent for only 40 years, reintroduction of large felids resulted in a 200% increase in vigilance of impala and wildebeest within a five-month period (Hunter and Skinner 1998). Berger et al. (2001) found that predator-naïve moose whose calves were killed by wolves colonizing Jackson Hole, Wyoming elevated vigilance response to wolf calls by about 500%. In this case, prey had been unfamiliar with dangerous predators (wolves) for as few as 50 to 130 years. In both studies, behavioral adjustments in response to increased predation transpired within a single generation.

Behavioral response of bighorn sheep to mountain lions in the Delamar Range was not of the same magnitude as observed in the examples above (Hunter and Skinner 1998; Berger et al. 2001). In the Delamar Range, behavioral adjustments took place within two
years after sheep were released, but the increase in vigilance was conditional. Instead of an overall increase in mean vigilance, adjustment of vigilance behavior occurred only in small groups of sheep foraging away from escape terrain. These results are inconsistent with predictions of an immediate and complete plastic adaptive adjustment of mean vigilance and mean norms of reaction for vigilance to increased predation risk. Further, they suggest that more time is required for exposure to lions before (1) further plastic adjustment can take place through learning, or (2), given existing heritability in the population, mean vigilance can evolve as a response to selection.

Vigilance of Ewes in Zion N. P.

The greatest amount of divergence in overall mean vigilance and in the degree of adjustment in covariance of vigilance with ecological variables was found in Zion N.P., the oldest translocated population (22 yrs). In Zion N.P., mean vigilance of ewes foraging in small groups, averaged across terrain types, was significantly higher than in the River Mountains. Mean vigilance (averaged across terrain types) of ewes in medium and large groups was also higher than in the River Mountains, but the difference was not significant. Divergence of mean norms of reaction for vigilance expressed across group size and terrain type occurred at both small and medium group sizes. Mean vigilance of bighorn ewes foraging in small and medium groups on both terrain types (on or near escape terrain verses away from escape terrain), was significantly higher than that of ewes in the River Mountains.

If the response of ewes in Zion N.P. was an entirely plastic response, behavioral adjustments could have occurred immediately for all individuals, or the increase might have occurred over time due to cultural or maternal learning in response to predator
encounters. It is also possible that the increase in vigilance was an evolutionary response to natural selection in the Zion N.P. population. Mean norms of reaction represent phenotypic mean responses of the population, and an increase or decrease in the slope of a population’s mean norm of reaction could indicate evolution of phenotypic plasticity (Carroll and Corneli 1999; Thompson 1999). The slope for mean norms of reaction for vigilance in River Mountains (source population) was zero; sheep in this population did not adjust vigilance in response to group size or in relation to escape terrain. In the Zion N.P. population, the slope for the norm of reaction for vigilance was strongly negative and significantly less than zero. Whether these observed changes in slope reflect genetic divergence of populations cannot be tested directly in this study. There are many examples of heritable variation in behavior (e.g., Dingle 1994; Lynch 1994; Travis 1994), and genetically based population differentiation in behavior (Carroll and Corneli 1999; Coss 1999; Reichert 1999; Thompson 1999). If genetic divergence in plasticity has evolved in transplanted populations, it would be dependent on the precondition that there was significant heritability of phenotypic plasticity or genotype by environment interaction (Carroll and Corneli 1999; Thompson 1999) in the founding populations.

Populations require time to respond to natural selection, and the length of time required for a response to selection is inversely related to the intensity of selection (Falconer 1989). If the observed adjustments in vigilance behavior are genetically based, then one could expect initial adaptive adjustments within one generation as the result of learned responses (observed in the Delamar population), followed by evolution of a heightened plastic response to predator encounters (heightened ability to learn) over generations, as seen in Zion N.P. If selection from mountain lion predation continues,
adaptive adjustments in vigilance for sheep in the Delamar Range would also be expected to increase over time with exposure to mountain lions, resulting in the evolution of a new degree of plasticity in vigilance for the population (evolution of the reaction norm) such that it would match the Zion N.P. population.

**Vigilance in the Pancake Range**

Patterns of vigilance behavior for sheep in the Pancake Range were not consistent with predictions of an optimal or adaptive hypothesis. Sheep in this population did not alter mean vigilance in response to group size. Contrary to expectations, there appeared to be little change in vigilance levels in response to increased predation. Although ewes in this population had higher vigilance levels than ewes in the River Mountains population, the difference was not significant. Indeed, behavioral responses of ewes, were the opposite of expected. When compared to the River Mountain population, ewes in the Pancake Range had significantly higher levels of vigilance when foraging on escape terrain compared to foraging away from escape terrain.

Bighorn sheep in the Pancake Range may not have adjusted vigilance in response to increased predation risk for a number of reasons. The length of time required for a response to selection is inversely related to the intensity of selection (Falconer 1989). If predation pressure from mountain lions was low, the population may not have had time to reach selective equilibrium for vigilance behavior. Even if observed divergence was a purely plastic response, predation might still be required as the cue or learning environment for a response in vigilance behavior. The number of sheep killed by lions in this mountain range is unknown, but there is evidence that mountain lions prey on sheep in this population. From the time sheep were first released, Nevada Department of...
Wildlife personnel reported seeing carcasses of sheep killed by lions (Pat Cummins, pers. comm.). Also, I observed mountain lion footprints in areas used by bighorn sheep during the course of this study, indicating that lions were still present in the mountain range.

If divergence in vigilance behavior of translocated populations is due to evolution of a heightened plastic response to predator encounters (heightened ability to learn) rather than a lag in learning, insufficient genetic variation in the founding population may have prevented the population from reaching adaptive optima (Foster and Endler 1999; Riechert 1999; Thompson 1999). Because founding populations are small (26 animals in the Pancake Range), the effects of genetic drift could also affect the response to selection (Falconer 1989). To understand how reintroduction affects genetic variability, Fitzsimmons et al. (1997) compared allozyme variability in four reintroduced populations of bighorn sheep with their common source population in Wyoming. In these populations, founder size (8-69) was low and effective population size ($N_e$) remained low ten to twenty years after release (Fitzsimmons et al. 1997). Simulations of genetic drift in translocated Rocky Mountain bighorn sheep populations indicated that although allele frequencies were within expectations of model predictions, heterozygosity sometimes varied from predictions. Although their results may have been influenced by small sample sizes, due to the difficulty of sampling small populations, genetic changes found in the reintroduced herds included shifts in allele frequencies, decreases in the numbers of alleles, and changes in heterozygosity (Fitzsimmons et al. 1997). Even if the requisite genetic variation exists within founding populations, selection on correlated characters could also slow or prevent adaptive differentiation (Price and Langen 1992). For
example, if selection for an increase in foraging efficiency is greater than the cost of increased vigilance, a tradeoff may occur.

Conclusions

The results presented in this chapter indicate that some, but not all, populations of bighorn sheep translocated from the River Mountains, an area lacking large predators, had the ability to respond to increased predation risk with an adaptive adjustment of vigilance behavior when translocated into habitat occupied by mountain lions. The magnitude of adaptive adjustment in vigilance behavior appeared to increase through time, from youngest to oldest transplant population. In the Delamar Range, behavioral adjustments took place within two years after sheep were released but the increase in vigilance was conditional. Instead of a plastic response resulting in an overall increase in mean vigilance and adaptive divergence of mean norms of reaction expressed across group size and escape terrain, divergence in vigilance behavior occurred only under conditions of highest perceived predation risk (small groups of sheep foraging away from escape terrain). These results are inconsistent with predictions of an immediate and complete plastic adaptive adjustment of mean vigilance to increased predation risk.

The greatest amount of divergence was found in the oldest translocated population. Bighorn ewes in Zion N.P. responded to increased predation risk with an overall increase in mean vigilance and an adaptive plastic adjustment in vigilance behavior relative to group size. This adaptive response was characterized by an increase in mean vigilance of bighorn ewes foraging in small and medium groups on both terrain types (on or near escape terrain versus away from escape terrain).
Patterns of response in the Delamar Range and Zion N.P. suggest that the amount of adaptive behavioral adjustment in vigilance may be positively correlated with duration of exposure to predators. Thus, in the Delamar Range, initial adaptive adjustments that occurred within one generation were the result of learned responses, while observed responses in Zion N.P could be due to evolution of a heightened plastic response to predator encounters (heightened ability to learn) that transpired over generations.

Behavioral adjustments did not, however, occur in all translocated populations. Sheep from the Pancake Range retained mean norms of reaction for vigilance that were similar to the River Mountains population. Although mean vigilance of ewes foraging away from escape terrain in the three selected group sizes was higher in the Pancake Range than in the River Mountains, the difference was not significant for small groups, which have the highest perceived predation risk. The nonadaptive response of ewes in the Pancake Range may have been due to little selection for increased vigilance because of low predation by mountain lions and/or genetic constraints.

Results from this chapter indicate that the observed lack of large-scale adaptation of vigilance, quantified in Chapter 2, is due, in part, to the nonadaptive response in vigilance observed in ewes from the Pancake Range. In addition, the variation in vigilance among the three replicate populations of native desert bighorn sheep with relaxed selection (Chapter 3) contributes to the overall pattern of non-adaptive geographic variation in vigilance. Given that some of the populations do exhibit adaptive norms of reaction for vigilance behavior, it appears that there are a variety of processes and contingencies that combine to generate the observed variability in behavior of bighorn sheep.
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CHAPTER 5

CONCLUSION

Studies presented in this volume test a variety of hypotheses about behavioral variation of vigilance in bighorn sheep populations. Because conflicting selective pressures frequently play an important role in shaping the evolution of ecologically important traits, individuals must balance conflicting demands (Shi 1987; Krebs and Davies 1996; Shi et al. 2003). Thus, models describing optimal vigilance assume a trade-off between the benefits of investment in predator detection and investment in other behaviors, particularly foraging (Lima and Dill 1990). In Chapter 2, as the first step in an assessment of geographic patterns of vigilance behavior in bighorn sheep, I tested the large-scale hypothesis that vigilance in bighorn sheep would differ between populations as a result of spatial heterogeneity in predation regimes. There was no difference in mean vigilance between bighorn sheep populations in habitat with low versus high predation risk. In light of these results, the large-scale hypothesis of an adaptive response of vigilance in populations of desert bighorn ewes under different predation risk was rejected. However, in habitat with predation risk from mountain lions, ewes did adjust vigilance in response to group size and terrain variables in a manner that was consistent with adaptive predictions.
In the third and fourth chapters, I addressed population differences in vigilance in the presence and absence of mountain lions to determine what conditions may have prevented large-scale adaptation. I examined norms of reaction for vigilance of the three native bighorn sheep populations inhabiting low-elevation mountain ranges without resident mountain lions to determine whether vigilance behavior in these populations reflects predicted patterns of adaptive or optimal behavioral plasticity in vigilance due to the costs of maintaining vigilance in the absence of predators. The results presented in Chapter 3 showed that the lack of fit to predicted patterns of adaptive vigilance between populations of bighorn sheep in habitat with resident mountain lions versus habitat without resident lions is at least partially due to variance of vigilance in response to relaxed selection in the three replicate populations of bighorn sheep in habitat without resident lions. This variance was attributed to the persistence of high mean vigilance levels despite relaxed selection in the Muddy and Eagle Mountain populations, and a non-adaptive or non-optimal plastic response of vigilance to group size and terrain type in the Muddy Mountains population. Vigilance behavior in the River Mountain population resembled predicted patterns of an adaptive or optimal response to relaxed selection, as did norms of reaction for vigilance expressed across group size and terrain type in the Eagle Mountains.

In Chapter 4, I compared changes in vigilance in populations of sheep translocated at different intervals of time from the River Mountains into habitat occupied by mountain lions to determine whether populations under relaxed predation pressure retained sufficient adaptive plasticity to adjust vigilance behavior in response to increased predation risk. The results presented in this chapter indicated that some, but not all,
populations of bighorn sheep translocated from the River Mountains, an area lacking large predators, had the ability to respond to increased predation risk with an adaptive or optimal adjustment of vigilance behavior when translocated into habitat occupied by mountain lions. The magnitude of adaptive or optimal adjustment in vigilance behavior appeared to increase through time, from youngest to oldest transplant population. In the Delamar Range, behavioral adjustments took place within two years after sheep were released but the increase in vigilance was conditional. Instead of a plastic response resulting in an overall increase in mean vigilance and adaptive divergence of mean norms of reaction expressed across group size and escape terrain, divergence in vigilance behavior occurred only under conditions of highest perceived predation risk; in small groups of sheep foraging away from escape terrain. These results were inconsistent with predictions of an immediate and complete plastic adaptive adjustment of mean vigilance to increased predation risk.

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Although it was not possible to test whether vigilance norms of reaction have evolved through natural selection, the use of reaction norms in this study provided a useful tool for understanding the structure of variation in vigilance behavior of desert bighorn sheep and provided a method of determining whether geographic patterns and covariation of
vigilance with group size and habitat were consistent with expectations of optimal behavioral allocation or adaptive behavioral plasticity.

What impact geographic variation in vigilance might have on the success of conservation efforts? One possible study to address this question is whether differences in reaction norms among source populations affect the success of translocations. Bighorn sheep in the Muddy Mountains are often used as founder stock in reintroduction efforts. Although overall vigilance in this population is high, it is also characterized by a nonadaptive or non-optimal response of vigilance to group size and terrain type. How successfully sheep translocated from this range adapt to a change in predation risk could in part, depend on whether behavioral differences are result of genetic diversification or from phenotypic plasticity.

Further studies to distinguishing the source of variation in vigilance are basic to understanding both the structure of adaptation within and among populations, and the process by which new behavioral phenotypes evolve. The opportunity to explore this and other details of anti-predator behavior under changing predation conditions are increasing as conservation efforts involving re-introductions continue. For example, the Pancake Range population has steadily increased since its establishment, and sheep from this population are now being considered as a source for additional translocations. The opportunity for a reciprocal transplant study may exist if sheep from this population are translocated into low elevation ranges without mountain lions.

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