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RESEARCH PAPER

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Persistence of antipredator behavior in an island population of California quail

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Abstract

Island populations may provide unique insights into the evolution and persistence of antipredator behavior. If antipredator behavior is costly and islands have reduced predation risk, then we expect the reduction or loss of antipredator behavior on islands. However, if even a single predator remains, the multipredator hypothesis predicts that antipredator behaviors will be conserved. We compared the flight initiation distances (FID) of California quail (*Callipepla californica*) on Santa Catalina Island (a location with reduced predation pressure) with quail on the mainland. We found no differences in FID between mainland and island quail. However, despite employing consistent testing methods, the starting distance from which quail were approached was significantly reduced for quail studied on the island when compared with quail studied on the mainland. Our results are consistent with the multipredator hypothesis because, while the island population had substantially fewer predators, some predators remained and some antipredator behavior persisted.

KEYWORDS
animal wariness, California quail, flight initiation distance, island tameness, isolation on islands, multipredator hypothesis, risk assessment

1 | INTRODUCTION

Many prey species lose costly antipredator behaviors when isolated on islands devoid of predators (Darwin, 1839). Such "island tameness" allows insular prey species to direct time and energy toward other important activities. New Zealand tammar wallabies (*Macropus eugenii*), for instance, showed a complete loss of antipredator behavior when isolated from all predators (Blumstein, Daniel, & Springett, 2004). Being isolated on an island also may be associated with a reduction or loss of antipredator behavior even if some predators are present. For instance, insular populations of lizards (Cooper, Pyron, & Garland, 2014) and macropodid marsupials (Blumstein & Daniel, 2005) had attenuated antipredator behavior. However, the loss of some predators does not always result in a complete reduction in antipredator behaviors and many species from diverse taxa maintain antipredator behavior when isolated from some, but not all predators (lizards on Aegean islands, Pafilis, Foufopoulos, Poulakakis, Lymberakis, & Valakos, 2009; yellow-bellied marmots (*Marmota flaviventer*; Blumstein, Ferando, & Stankowich, 2009), and Hokkaido deer (*Cervus nippon yesoensis*) living without wolves (*Canis lupus*; Osada, Miyazono, & Kashiwayanagi, 2015)).

Both the risk allocation (Lima & Bednekoff, 1999) and threat sensitivity (Helfman, 1989) hypotheses may explain "island tameness", noting that reduced predation risk leads to reduced antipredator vigilance and other forms of antipredator behavior. The risk allocation hypothesis states that temporal variation in predation risk drives antipredator behavior (Lima & Bednekoff, 1999). As overall predatory attacks increase, animals should allocate more vigilance in high-risk situations, but should allocate less vigilance in low-risk situations to make up for lost feeding (Lima & Bednekoff, 1999). However, the need to feed means that animals will become less vigilant in high-risk situations that span long periods of time (Lima & Bednekoff, 1999). Similarly, the threat sensitivity hypothesis states that prey will alter their antipredator response to reflect predatory threat levels (Helfman, 1989). Prey is expected to evade predators to a degree that reflects the magnitude of threat. For example, threespot damselfish (*Stegastes planifrons*) responded in graded fashion to varying threat levels, with antipredator response increasing with threat (Helfman, 1989). Distinguished primarily by the influence of the threat frequency on vigilant behavior, both the risk allocation and threat sensitivity hypotheses predict that prey will exhibit relaxed antipredator behavior on islands with reduced predation pressure.

Alternatively, the multipredator hypothesis may explain the persistence of antipredator behavior despite reduced predation pressure (Blumstein, 2006). Antipredator behavior, including predator-specific responses, can be genetically linked to other functional behaviors (Coss, 1999), and the loss of one or some predators should have a minimal effect on the independent assortment of these genes (Curio, 1973). For example, recognition systems that might be specific to a single predator may be linked and integrated with broader interspecific recognition strategies and, thus, the entire system would not be lost with the disappearance of a specific predator (Blumstein, 2006). Thus, the hypothesis predicts that the loss of one or some predators for species with multiple predators should not lead to a substantial decline in antipredator behavior as long as one or a few predators remain.

Flight initiation distance (FID), the distance at which a prey flees from an approaching predator or threat, is a metric used to study wariness in a variety of animals (Cooper & Blumstein, 2015). As FID has shown to be influenced by many of the same factors that contribute to an animal's wariness, including group size (Burger & Gochfeld, 1991), distance to cover (Dill & Houtman, 1989), and season (Richardson & Miller, 1997), both biologists and wildlife managers regularly use FID as a metric of fear (Blumstein, Anthony, Harcourt, & Ross, 2003). We compared the FIDs of California quail (*Callipepla californica*) studied on Santa Catalina Island to quail studied on the California mainland. Optimal flight initiation distance maximizes prey fitness, by balancing the foraging costs of fleeing too early while danger is still low, against the risk of death from fleeing too late from a predator (Cooper, 2015). Therefore, an increase in predation risk (or the diversity of predators) should result in an increase in wariness and thus increased FID (Cooper & Frederick, 2007). Furthermore, it has been shown that, as distance from the mainland increases, FID decreases in lizards (Cooper et al., 2014). This suggests that the 47.1 km gap that isolates the island and has led to the reduction in predators compared to the California mainland will likely lead to shorter island FIDs.

Predictions from the risk allocation, threat sensitivity, and multipredator hypotheses were tested by comparing populations on an island with fewer predators to populations living on the mainland with a full complement of predators (Table 1). While both the risk allocation and threat sensitivity hypotheses predict a shorter FID in insular quail, the multipredator hypothesis predicts no changes in FID due to the presence of some predators. The island-associated reduction in predation threat due to substantially fewer predator species, as well as smaller predator populations compared to the mainland, make California quail an ideal study species for testing

TABLE 1 California Quail Predators

Predator[a]	**Mainland**	**Island**
Class: Aves		
American crow (*Corvus brachyrhynchos*)[b]	•	•
American kestrel (*Falco sparverius*)	•	•
Bald eagle (*Haliaeetus leucocephalus*)	•	•
Common raven (*Corvus corax*)[b]	•	•
Cooper's hawk (*Accipiter cooperii*)	•	
Great horned owl (*Bubo virginianus*)	•	
Greater roadrunner (*Geococcyx californianus*)[b]	•	
Northern harrier (*Circus cyaneus*)	•	
Northern pygmy owl (*Glaucidium gnoma*)	•	
Prairie falcon (*Falco mexicanus*)	•	
Peregrine falcon (*Falco peregrinus*)	•	
Red-tailed hawk (*Buteo jamaicensis*)	•	
Scrub jay (*Aphelocoma californica*)	•	
Sharp-shinned hawk (*Accipiter striatus*)	•	
Class: Mammalia		
Black rat (*Rattus rattus*)[b]	•	•
Bobcat (*Lynx rufus*)[b]	•	
California chipmunk (*Tamias obscurus*)[b]	•	
California ground squirrel (*Otospermophilus beecheyi*)[b]	•	
Catalina Island fox (*Urocyon littoralis catalinae*)[c]		•
Coyote (*Canis latrans*)[b]	•	
Feral cat (*Felis catus*)[b]	•	•
Gray fox (*Urocyon cinereoargenteus*)[b]	•	
Long-tailed weasel (*Mustela frenata*)	•	
Raccoon (*Procyon lotor*)[b]	•	
Red fox (*Vulpes vulpes*)	•	
Striped skunk (*Mephitis mephitis*)[b]	•	
Virginia opossum (*Didelphis virginiana*)	•	
Class: Reptilia		
California kingsnake (*Lampropeltis getula californiae*)[b]	•	•
California mountain kingsnake (*Lampropeltis zonata*)[b]	•	
Gopher snake (*Pituophis catenifer*)[b]	•	•
Southern Pacific rattlesnake (Crotalus oreganus helleri),	•	
Rattlesnake and other snakes[b]	•	

[a] Glading, 1938; Emlen & Glading, 1945; Leopold, 1977; Fielder, 1982; Alhborn, 1990; Shuford, 1993; Golightly, Faulhaber, Sallee, & Lewis, 1994; Klauber, 1997; Guttilla, 2007; Calkins, Gee, Hagelin, & Lott, 2014.

[b] nest predators.

[c] Whether Island foxes eat quail is unclear, but scat analyses across all six Channel Islands suggest that birds comprise less than 5% of Catalina Island fox diets (Cypher et al., 2014). Although this could indicate that the foxes do feed on quail occasionally, birds ultimately comprise an insignificant portion of island fox diets and would therefore not be common predatory targets.

the key predictions of the risk allocation and threat sensitivity vs. multipredator hypothesis.

2 | MATERIALS AND METHODS

2.1 | Study site and subjects

California quail are ground-dwelling New World pheasants that congregate in groups, known as coveys, which can range in size from two to thousand birds, but average fifty individuals (Calkins, 2007; Leopold, 1977). Quail were likely introduced to Catalina Island about 12,000 years ago by Native Americans, and there is minimal genetic divergence between island and mainland quail populations (Zink, Lott, & Anderson, 1987).

We quantified fight initiation distance on Santa Catalina Island during Oct. 2016 and on the California mainland between Feb. and Apr. 2017. Although quail typically pair off during the nesting season, which begins in late March (Lewin, 1963), only birds congregated outside of nesting sites, within coveys, were tested. Both mainland and island birds were in coastal and oak chaparral habitat where hunting was prohibited (Table S1). The chaparral plant community was mainly composed of chamise (*Adenostoma fasciculatum* and *Adenostoma rosaceae*), scrub oaks (*Quercus pacifica* on Catalina; *Quercus berberidifolia* on mainland), native and non-native grasses no taller than two feet high (Poaceae), low shrubland plants such as coastal sage scrubs, and coastal prickly pear (*Opuntia littoralis*) on Catalina (Backs & Ashley, 2016; Griffin, 1995; Haggerty & Mazer, 2010; Hein & de la Rosa, 2013). Quail in our experiment was almost always in open clearings surrounded by these shrubs and plants. We only performed experiments and observations when we had an unobstructed approach to quail as we found them in their environment.

2.2 | Quantifying flight initiation distance

To conduct FID tests, we identified a "relaxed" individual quail (foraging, preening, or walking; Blumstein, 2003). The observer walked toward the focal individual at a speed of 0.5 m/s and measured three distances: the starting distance (SD), the alert distance (AD), and FID. Starting distance measured the distance between the observer and the focal individual when the observer initiated approach. If the focal subject was not relaxed, the observer increased SD and waited until the individual or covey was relaxed before initiating approach. To avoid any potential bias in SD, the observer only flushed birds that were grazing in clearings, free from any obstacles that might obstruct the observer's approach or cause the observer to start closer or further away. Alert distance measured the distance the focal individual became alerted to the approaching observer by orienting its head toward the observer. Finally, FID measured the distance the focal individual became fled the approaching observer. We measured SD, AD, and FID using a rangefinder with a 100-meter range. Because quail rarely fly, their evasive behavior did not always involve winged flight; thus, escape as defined in our study included walking away from the observer. To avoid resampling, at each study site, we performed tests at different locations and at different times of the day and believe we identified individuals in different coveys. Even if occasional resampling occurred, modest resampling has little effect on FID studies (Runyan & Blumstein, 2004).

2.3 | Statistical analyses

We $\log_{10}$ transformed FID and SD to normalize and homogenize the variances of the distribution of these variables after Levene's tests revealed heterogeneity of variance. We examined variation in FID by fitting a general linear model with covey size (CS), SD, location (island/mainland), and the interaction between SD and location (island/mainland). Although we measured both SD and AD (when possible), only one variable is needed for analysis because SD and AD are highly correlated. We did not include AD as a covariate in our model because AD was difficult to determine for some of our approaches. In addition, we compared $\log_{10}$ SD on the island and mainland populations with a *t* test to test for differences in SD. We report the adjusted R^2 of the general linear model, partial eta squared as a measure of effect size, and set our alpha to 0.05. We conducted all statistical tests using SPSS (v 24–IBM 2017).

3 | RESULTS

We flushed 32 individuals on the mainland and 34 on the island. After $\log_{10}$ transformation, the variance in FID on the island and mainland was not significantly different (Levene's test $p = .41$). Our model (Table 2) explained approximately 58% of the variation in $\log_{10}$ FID as a function of $\log_{10}$ SD, location (island/mainland), covey size, and the interaction between SD and location. FID was not significantly influenced by location or covey size, or the effect of SD as a function of location, but was significantly influenced by SD only (Table 2). A *t* test ($t = 2.29$; $p = .02$) further revealed significantly shorter $\log_{10}$ SD on the island ($X \pm SD = 1.41 \pm 0.32$ m) compared to the mainland ($X \pm SD = 1.57 \pm 0.22$ m).

4 | DISCUSSION

Our results are consistent with the multipredator hypothesis (Blumstein, 2006), which predicts that the presence of any predator

TABLE 2 Factors explaining variation in California quail flight initiation distance

Source	Unstandardized coefficient (B)	*p*-value	Partial eta squared
Corrected Model[a]		**<.001**	0.60
Intercept	0.02	.57	0.01
Location (Island)	0.12	.68	0.00
Log_{10} Covey Size	0.06	.27	0.02
Log_{10} SD	0.76	**<.001**	0.48
Location (Island)*$\log_{10}$ SD	−0.11	.54	0.01

[a] Adjusted R squared = 0.575. Significant *p*-values are bold.

will maintain fully expressed antipredator behaviors in prey populations that have lost some but not all predators. Additionally, our results contradict key predictions from both the risk allocation (Lima & Bednekoff, 1999) and threat sensitivity (Helfman, 1989) hypotheses. Many of the carnivores present on the mainland are absent on Catalina Island, and thus, quail should experience some degree of relaxed selection for escape behaviors. However, there is a reduced complement of both aerial and terrestrial predators on Catalina Island and this seems to be sufficient to maintain the same level of wariness on the island as seen on the mainland.

The 12,000-year history of quail on Catalina Island makes it unlikely that the birds will lose this response in the future as long as some predatory threats remain on the island (Collins, 2008; Zink et al., 1987). Because antipredator genes are likely linked, the loss of some predators may not affect the antipredator responses for other predators (Blumstein, 2006). As the loss of costly behaviors may occur rapidly (50–70 years in moose at the Rocky Mountains and Alaska's Cook Inlet–Berger, 1999; 25 years in moose at Alaska's Kenai Peninsula–Pyare & Berger, 2003; ≤130 years in tammar wallabies–Blumstein et al., 2004; one generation in captive birds–Carrete & Tella, 2015), if an island effect (Cooper et al., 2014; Darwin, 1839) were at play, the results of such an effect should be apparent in this study (Berger, Swenson, & Persson, 2001).

While FID was not significantly different between the two populations, the SD differed; we began to approach relaxed insular quail at closer distances. Although it may seem that SD is determined by the predator, it is also partly determined by the prey as well as habitat openness and visibility (Samia et al., 2017). Importantly, we used identical methods when flushing quail in both locations and it was necessary for us to increase our SD from quail that required a longer distance to be relaxed before experimentation. As habitat, or habitat openness, did not differ in any obvious way and quail were found in similar oak chaparral both on the island and on the mainland, we suspect the shorter SD in insular birds is due to reduced wariness of approaching predators, but not enough such that FID is also shorter. However, there is no previous evidence to suggest that SD (among other escape-related variables) is indicative of antipredatory response strength and our findings support further investigation. SD is positively correlated with FID (Blumstein, 2003; Cooper, 2005; Cooper & Sherbrooke, 2015; Fleming & Bateman, 2017; Møller, 2012; Stankowich & Coss, 2006), and the flush early hypothesis explains that earlier predator detection increases the need to monitor an approaching predator, causing prey to flush early to reduce this cost (Blumstein, 2010; Chamaillè-Jammes & Blumstein, 2012; Cooper, 2015).

The retention of antipredator behavior in quail despite the reduced predation on Catalina Island is consistent with a study on Catalina Island orange-crowned warblers (*Oreothlypis celata*) that showed that the presence of predatory ravens on an island otherwise devoid of avian nest predators allowed the retention of antipredator behavior when tested against experimental model predators (Peluc, Sillett, Rotenberry, & Ghalambor, 2008). Furthermore, Island scrub jays (*Aphelocoma insularis*) maintained egg rejection as a defensive behavior against brood parasitism in the absence of brood parasites on the island (Peer, Rothstein, Delaney, & Fleischer, 2007), supporting the idea that defensive behaviors can be maintained following the loss of a threat. However, our results are inconsistent with a study showing increased exploratory activity in Island scrub jays in comparison with mainland California scrub jays (*Aphelocoma californica*), but this may possibly be explained by food shortages in addition to reduced predation on the island (Haemig, 1988). Further studies on risk assessment may clarify the causes of such discrepancies.

Future work should focus on determining factors that may explain differences in SD, but not flight initiation distance, between populations with differing predation threats, including increased urbanization (Samia et al., 2017). Regardless, our results add to a growing body of literature that supports the multipredator hypothesis. For systems where the hypothesis applies, the multipredator hypothesis has important implications for wildlife conservation and management because it gives us the tools to predict the conditions under which escape behaviors will be maintained following the loss and reintroduction of predators.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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