



Change In Merlin Hunting Behavior Following Recovery of Peregrine Falcon Populations Suggests Mesopredator Suppression

Author: Buchanan, Joseph B.

Source: Journal of Raptor Research, 46(4) : 349-356

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/JRR-11-75.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

CHANGE IN MERLIN HUNTING BEHAVIOR FOLLOWING RECOVERY OF PEREGRINE FALCON POPULATIONS SUGGESTS MESOPREDATOR SUPPRESSION

JOSEPH B. BUCHANAN¹

Cascadia Research, 218½ West Fourth Avenue, Olympia, WA 98501 U.S.A.

ABSTRACT.—Relationships between apex predators and mesopredators have been poorly documented in predatory birds. Prediction from intraguild predation (IGP) theory suggests that following the recovery of Peregrine Falcon (*Falco peregrinus*) populations, the potential for Merlins (*F. columbarius*) to experience mesopredator suppression should increase where these species share habitat and prey resources. In Washington, both falcons prey on Dunlins (*Calidris alpina*) in estuarine ecosystems during the nonbreeding season. To investigate whether mesopredator suppression may have occurred, I compared aspects of the hunting behavior of Merlins at an estuary in western Washington between 1999 and 2009, when Peregrine Falcons were regularly present, with hunting behavior in the 1980s, when Peregrine Falcons did not occur at the site. Merlin hunting behavior changed substantially between the two periods. Following Peregrine Falcon recovery, Merlins hunted less frequently, used hunting flights of shorter duration and that involved fewer capture attempts per successful flight, and captured prey closer to the cover of vegetation, results that are consistent with IGP theory. Prior to Peregrine Falcon recovery, Merlins appear to have assumed the role of apex falcon predator at the site; Merlins currently coexist with Peregrine Falcons, and have altered their hunting behavior which may reduce their risk of IGP.

KEY WORDS: *Merlin; Falco columbarius; Peregrine Falcon; Falco peregrinus; hunting behavior; intraguild predation; mesopredator suppression; Washington; winter.*

EL CAMBIO EN EL COMPORTAMIENTO DE CAZA DE *FALCO COLUMBARIUS* LUEGO DE LA RECUPERACIÓN DE LAS POBLACIONES DE *FALCO PEREGRINUS* SUGIERE LA SUPRESIÓN DEL DEPREDADOR INTERMEDIO

RESUMEN.—Las relaciones entre los depredadores tope y los depredadores intermedios han sido poco documentadas en las aves depredadoras. Una predicción de la teoría de la depredación intra-gremio (DIG) sugiere que luego de la recuperación de las poblaciones de *F. peregrinus*, *F. columbarius* en condición de depredador intermedio debería experimentar una disminución en aquellos lugares donde estas especies comparten recursos de hábitat y presas. En Washington, ambos halcones cazan *Calidris alpina* en ecosistemas estuarinos durante la época no reproductiva. Para investigar si la supresión del depredador intermedio podría haber ocurrido, comparé aspectos del comportamiento de caza de *F. columbarius* en un estuario del oeste de Washington entre 1999 y 2009, cuando individuos *F. peregrinus* estuvieron presentes regularmente, con el comportamiento de caza en la década de 1980, cuando *F. peregrinus* no se encontraba en el sitio de estudio. El comportamiento de caza de *F. columbarius* cambió sustancialmente entre estos dos periodos. Luego de la recuperación de *F. peregrinus*, *F. columbarius* cazó con menor frecuencia, empleó vuelos de menor duración que implicaron menos intentos de captura por vuelo exitoso y capturó sus presas más cerca de la cubierta de la vegetación, resultados que son consistentes con la teoría de DIG. Antes de la recuperación de *F. peregrinus*, *F. columbarius* parecía haber asumido el rol de halcón depredador tope en el sitio. Actualmente *F. columbarius* coexiste con *F. peregrinus*, y ha alterado su comportamiento de caza, lo que puede reducir su riesgo de DIG.

[Traducción del equipo editorial]

When apex predators are removed from a community, other predators may subsequently respond functionally or numerically to this change, a phenomenon

known as mesopredator release (Soulé et al. 1988). The “release” of mesopredators occurs when the controlling effects of competitive or predator interactions with the dominant predator are removed. Some mesopredators functionally ascend to apex predator

¹ Email address: Joseph.Buchanan@dfw.wa.gov

status following mesopredator release (Prugh et al. 2009). Conversely, when top predators enter communities from which they had been absent, responses by lower predators may reflect a mesopredator suppression effect.

A predator-prey relationship between two predator species which share a resource (e.g., prey) is referred to as intraguild predation (IGP), a widespread and relatively common phenomenon among mammals (Polis et al. 1989, Polis and Holt 1992, Palomares and Caro 1999, Arim and Marquet 2004) and raptors (Petty et al. 2003, Sergio and Hiraldo 2008, Zuberogoitia et al. 2008, Chakarov and Krüger 2010). Mesopredator raptors also appear to respond behaviorally to the presence of raptors that are capable of killing them, and aspects of avoidance behavior during the breeding season, as evidenced by patterns of space use or territory occupancy, have been reported (e.g., Hakkarainen and Korpimäki 1996, Sergio et al. 2003, 2007, Sergio and Hiraldo 2008, Zuberogoitia et al. 2008).

Throughout much of its nearly global distribution, Peregrine Falcon (*Falco peregrinus*) populations declined due to the effects of chemical contaminants following World War II (Cade et al. 1988). A multi-decade effort eventually resulted in recovery of Peregrine Falcon populations throughout North America and elsewhere (White et al. 2002). Peregrine Falcons prey on a wide variety of bird species (White et al. 2002), including shorebirds (Dekker 1980, 1988, Buchanan 1996). Merlins (*F. columbarius*) also prey on shorebirds (Page and Whitacre 1975, Dekker 1988, Buchanan 1996), and use estuarine habitats throughout much of the Peregrine Falcon's winter range in North America (Warkentin et al. 2005). The Peregrine Falcon is both a competitor (Dekker 1980, 2003, Palmer 1988) and potential predator of the Merlin (Ratcliffe 1980, Palmer 1988, Zuberogoitia and Prommer 2011). Consequently, Merlins might be expected to experience mesopredator suppression following the recovery of Peregrine Falcon populations. Indeed, at the Kennedy Creek estuary in western Washington, during winters between 1980 and 1988, a period prior to Peregrine Falcon recovery, Merlins were regularly present, whereas the latter species was observed less frequently between 1999 and 2005, when Peregrine Falcons had begun to use (or reuse) the site (Buchanan 2009), suggesting a behavioral manifestation of mesopredator suppression.

Taking advantage of a "natural experiment"—facilitated by the recovery of Peregrine Falcon populations

during the late twentieth century—I investigated whether Merlin hunting behavior had changed in a manner consistent with that expected if mesopredator suppression had occurred. Specifically, I assessed the potential existence of mesopredator suppression by comparing hunting behavior and performance of Merlins both prior to and following Peregrine Falcon recovery.

STUDY AREA

The study was conducted at Kennedy Creek estuary in south Puget Sound, Washington, U.S.A. (47°5.83'N, 123°4.82'W). The estuary includes a 7.7-ha saltmarsh of native vegetation and is within the Kennedy Creek Natural Area Preserve (Brennan et al. 1985, Zukerberg and Pearson 2006). The marsh is at the southern terminus of the inlet and mudflats extend northward. The adjacent or nearby uplands are dominated by Douglas-fir (*Pseudotsuga menziesii*) forests mostly ~50 yr in age. These forests extend to the shore on both sides of the inlet, which is about 800–900 m from side to side. Vegetation cover did not change appreciably during the study period. The climate during winter is cool and wet, with precipitation occurring primarily as rain, and temperatures generally >0°C.

Despite its relatively small size, the study area regularly supported falcons and substantial numbers of shorebirds. It was not possible to determine the actual number of Merlins using the site during the study, although multiple birds were simultaneously observed on several occasions and individuals of various age and sex classes of the *F. c. columbarius* and *F. c. suckleyi* subspecies were observed (Buchanan et al. 1988b; J. Buchanan unpubl. data), indicating the hunting behavior I observed reflected that of numerous falcons. Peregrine Falcons were not observed during winter in the 1980s, but between 1999 and 2010 they began using the site and were observed more frequently than Merlins (see Buchanan 2009). All hunting flights by Merlins were directed at Dunlins (*Calidris alpina*), which made up ≥95% of the winter sandpiper community (Buchanan 1988a, Evenson and Buchanan 1997, J. Buchanan unpubl. data), with between 1500 and 5000 Dunlins typically present (Buchanan 1988a, J. Buchanan unpubl. data).

METHODS

Observations of Hunting Behavior. I observed falcon hunting behavior between November and mid-April as part of a long-term shorebird monitoring

project. I made 114 visits to the site in the years 1981–88 and 397 visits in the years 1999–2010; I made few visits between those periods and did not include data from the intervening years in the analyses. My visits to the site occurred during all phases of the tidal cycle in which mud flats were exposed diurnally. I observed falcon hunting behavior by: (1) noting the predator-evasion behavior of shorebirds to indicate the possible presence of a falcon, (2) seeing the falcon in flight before or during an attack on prey, and (3) checking several perches known to be used by falcons, although the last technique was rarely successful.

When Merlins hunted shorebirds, I recorded information on various aspects of their behavior. For each hunting flight, I recorded the duration of the flight (in 1-min time intervals), the location of prey capture, the number and type of capture attempts (e.g., stoop [a dive at the flock that, depending on its origin, could be nearly vertical or of a lesser angle], horizontal pass, tail-chase; see Buchanan et al. 1988b), and whether the hunting flight was successful. In the 1980s, prey capture locations were recorded as estimated distances and general bearings from my position, whereas those from the recent study period were described in notes and marked on a map for later distance measurements. A *hunting flight* was defined as a flight—generally perch-to-perch, but also those with unknown beginning and/or endings—that was directed at Dunlins. All hunting flights by definition included at least one capture attempt. A *capture attempt* was defined as an obvious attempt to capture prey, as evidenced by the falcon approaching the Dunlin close enough that a capture appeared imminent. Terminology and definitions used to categorize falcon behavior (Buchanan et al. 1988b) were the same in both study periods.

Statistical Analyses. If the presence of Peregrine Falcons influenced aspects of the behavior of Merlins, null hypotheses would posit no differences in Merlin behavior between the 1980s and the 1999 to 2010 study periods. A previous analysis evaluated the occurrence of Merlins at the study site between 1999 and 2005, compared to the 1980s, when Peregrine Falcons were absent (Buchanan 2009). The present analyses therefore focus on other aspects of Merlin behavior.

The 1980s phase of this study originally included several estuarine study areas in western Washington (Buchanan et al. 1988b). In contrast, the effort from 1999 to 2010 occurred exclusively at Kennedy Creek

estuary. To eliminate site-effects, for the 1980s study period I used Merlin behavior data collected only at Kennedy Creek estuary ($n = 114$ site visits).

Prior to all analyses, I evaluated data distributions using the Shapiro-Wilk normality test. When two-sample t -tests could not be used because data were non-normally distributed, I used the Mann-Whitney U -test.

Relative to the occurrence of hunting Merlins, I conducted two analyses of the incidence of Merlin hunting flights. In the first analysis, I compared the mean amount of field time per observation of a hunting flight per season from both periods to assess the relative occurrence of hunting Merlins during the nonbreeding period. The second analysis differed by including only those days when Merlins were observed at the site, which reflects the frequency with which Merlins hunted on days they were confirmed present at the site.

If Merlins were wary of Peregrine Falcons and tended to avoid them, Merlins should have exhibited risk-averse behavior when hunting in habitats shared with the larger falcon. Consequently, I evaluated specific elements of hunting behavior that might indicate risk-aversion. The number of capture attempts made per hunting flight may indicate a Merlin's risk aversion during a hunting flight if the Merlin is aware of the risk of being robbed or attacked after expending considerable energy while hunting (Buchanan 1988b). Therefore, I compared the number of capture attempts per hunting flight in both study periods. I also evaluated whether there were differences in the duration of successful and all hunting flights (<1 min versus ≥ 1 min), using the Fisher exact test in the analysis of successful flights due to the small sample size. Similarly, the stoop is a more conspicuous hunting behavior than a low-stealth approach flight, and is more likely to advertise a Merlin's presence to a nearby Peregrine Falcon than the latter. I therefore compared the proportions of hunting flights that included at least one stoop.

I compared the outcome and location of Merlin hunting flights from the 1980s with those between 1999 and 2010. I compared the proportions of: (1) successful hunting flights, (2) successful capture attempts, and (3) hunting flights that were successful on the first capture attempt. Lastly, I evaluated the proximity of prey captures to vegetation cover by testing the hypothesis that there was no difference in prey capture location distance from cover between the two study periods.

RESULTS

The occurrence of Merlin hunting activity changed between the two study periods. In the 1980s, I observed 74 hunting flights by Merlins, at a mean annual rate of one hunting flight per 265.3 min (SD = 188.8) afield over nine winters. This was a significantly greater rate than that for 10 winters between 1999 and 2010, when 27 hunting flights were observed at a rate of one hunting flight per 1374.5 min (SD = 1021.4; Mann-Whitney $U = 95$, $P < 0.001$). On days when Merlins were observed at the site, the mean annual rate of hunting flights was one per 75.4 min (SD = 53.9) in the 1980s and one per 118.1 min (SD = 79.6; $t = 1.31$, $P = 0.21$) in 1999 to 2010, suggesting that when Merlins were confirmed to be present in either period there was no difference in the likelihood they would hunt or be detected hunting.

Other aspects of Merlin hunting behavior changed in a manner consistent with a mesopredator suppression effect. In contrast to the 1980s, when 30 of 69 (43.4%) hunting flights where time was recorded were <1 min in duration, in 1999 to 2010, 22 of 27 flights (81.5%) lasted <1 min (test of proportions, $Z = 3.36$, $P < 0.001$). Eleven of 12 (91.7%) successful hunting flights in 1999 to 2010 lasted <1 min, compared to only 4 of 12 (33.3%) successful hunting flights in the 1980s (Fisher exact test, $P = 0.009$). In addition to their shorter duration, successful hunting flights in 1999 to 2010 had fewer capture attempts (mean = 1.3, SD = 0.89) compared to successful flights in the 1980s (mean = 5.5, SD = 6.4; Mann-Whitney $U = 118$, $P = 0.004$). Use of a conspicuous hunting method, the stoop, did not differ, as they constituted 43.5% of the capture attempts in both periods (test of proportions, $Z = 0.36$; $P = 0.99$).

Success rates of hunting activities changed substantially between the two study periods. The success rate of Merlin hunting flights in the 1980s was much lower (12 successes in 74 flights; 16.2%) compared to that in 1999 to 2010 (12 of 27; 44.4%; test of proportions, $Z = 2.95$, $P = 0.003$). Consistent with this finding, the success rate of capture attempts was lower in the 1980s (12 of 264 capture attempts; 4.5%) than in 1999 to 2010 (12 of 46; 26.1%; test of proportions, $Z = 5.04$, $P < 0.001$). Finally, 3 of 12 (25%) hunting flights in the 1980s were successful on the first capture attempt, in contrast to 1999 to 2010, when 10 of 12 (83%) were successful on the first attempt (Fisher exact test, $P = 0.012$).

The locations of prey captures changed between the two study periods. The median distance of 12 prey captures from vegetation cover between 1999 and 2010 was 49 m and was significantly less than that of 12 prey captures in the 1980s (262.5 m; Mann-Whitney $U = 43$, $P = 0.057$). Nine of 12 recent captures were <110 m from vegetation cover and seven of these were <50 m from cover in the recent period. Most captures in the 1980s occurred over the middle of the inlet (above exposed mud or open water) and were generally hundreds of meters from cover.

DISCUSSION

The release of mesopredators can occur very rapidly (Henke and Bryant 1999, Prugh et al. 2009) and can result in behavioral changes that include mesopredator ascendancy to apex predator status (Gese and Grothe 1995). In the 1980s, Merlins regularly hunted over the center of the inlet, often using a high, conspicuous flight over the inlet where the falcon would then stoop at Dunlin flocks or tail-chase individuals, sometimes engaging in flights lasting several min (Buchanan et al. 1988b), behavior somewhat similar to that noted in hunting flights by Peregrine Falcons (Buchanan et al. 1986). The highly synchronous flight behavior used by Dunlins to avoid predation made these encounters conspicuous (Buchanan et al. 1988b), and likely visible to other avian predators in the vicinity. Given the rarity of these hunting tactics between 1999 and 2010, it appears that in the absence of Peregrine Falcons during the 1980s, Merlins exhibited behavior suggesting ascendancy to the role of apex falcon predator.

Mesopredator suppression is expected to occur when an apex predator enters an ecosystem or community, including one which it had formerly occupied, and can be manifested in a variety of changes directly or indirectly resulting from the presence of the apex predator. Although the design of my project did not allow for establishing cause-and-effect relationships, several key aspects of Merlin hunting behavior and performance changed between the 1980s, when Peregrine Falcons were absent, and the 1999 to 2010 period, when Peregrine Falcons were present. Consistent with a mesopredator suppression effect, the rate of Merlin occurrence decreased between the two periods (Buchanan 2009), as did the rate at which they were observed hunting. Similarly, hunting flights in the recent period, including those that resulted in prey capture, were shorter in duration and included fewer capture

attempts. Finally, recent prey captures by Merlins occurred closer to potential escape cover than those from the 1980s, and only three captures occurred far from cover, in the general area where many captures occurred during the 1980s.

Given that changes in Merlin hunting activity largely consistent with a mesopredator effect occurred following Peregrine Falcon recovery, it initially seemed counter-intuitive that the Merlin's hunting efficiency increased rather than declined in the latter period. When an apex predator is present, the suppression of mesopredators can be directly or indirectly linked to the apex predator (Lima 1998, Berger et al. 2008, Peckarsky et al. 2008). A direct effect occurs when an apex predator kills a mesopredator, whereas an indirect, nonlethal, or nonconsumptive effect occurs when the apex predator's presence influences the ecology or behavior of the mesopredator or its prey (Lima 1998, Peckarsky et al. 2008, Zuberogotia et al. 2008).

According to IGP theory, when two predator species—the IG predator (apex; Peregrine Falcon) and the IG prey (mesopredator; Merlin)—rely on a shared prey species, coexistence is possible only if the IG prey is the superior competitor for the shared resource (Holt and Polis 1997). In my study, the IG prey was equivalent to, if not more, effective (hunting success rate = 44.4%) than the IG predator in terms of hunting success (14 captures in 44 hunting flights during the recent study period, for a success rate of 31.8%; J. Buchanan unpubl. data). Additionally, IG predators are expected to directly or indirectly exclude IG prey from highly productive systems (Holt and Polis 1997). Although many exceptions to the latter theory component have been reported (Amarasekare 2008), it is difficult to reconcile the lack of competitive subordination of the IG prey in the presence of the IG predator. Specifically, why is Merlin hunting efficiency higher after the reestablishment of the Peregrine Falcon as a winter resident of the study area compared to the 1980s when the latter species was absent? Two scenarios seem plausible and each can be evaluated to some extent with additional field data.

Under the first scenario, Peregrine Falcons would kill or in some way exclude Merlins from the site. Peregrine Falcons are known to capture and kill smaller falcons (Palmer 1988). If unwary Merlins are unable to consistently recognize the presence or potential threat of a Peregrine Falcon, they would be at risk of predation. Merlins unable to effectively adapt their hunting behavior could reduce their risk

by shifting their hunting activities to areas distant from those used by Peregrine Falcons (Kostrzewa 1991, Durant 1998). This would potentially magnify behavioral trends of the remaining Merlins that did adapt to the presence of Peregrine Falcons, perhaps reflecting age-related differences in hunting success (Orians 1969), if, for example, adult Merlins were more efficient predators than juveniles.

Under the second scenario, the addition of Peregrine Falcons could reduce the vigilance of the shared prey (Dunlin) such that they are more vulnerable to capture by Merlins. In a recent model, Kimbrell et al. (2007) found that when an IG predator attacks IG prey, competition is directly or indirectly reduced for the IG predator and vigilance by the shared prey is also reduced; density reduction of the IG prey was identified as the mechanism for reduced vigilance by the shared prey. This model, however, was based on an IG prey with inefficient hunting skills, which appears to be untrue of Merlins (Buchanan et al. 1988b, this study). An IGP meta-analysis indicated an overall pattern of prey release in response to the addition of an IG predator to a system, although an analysis specific to terrestrial vertebrates indicated multi-predator prey suppression when an IG predator was added to the system (Vance-Chalcraft et al. 2007). An investigation of the vigilance of shared prey has not been conducted at my study site, but it is conceivable that Dunlins have become less vigilant for IG prey if: (a) they were primarily vigilant for the IG predator, which seems possible, or (b) there was a reduced density or occurrence of Merlins, which despite an increased hunting efficiency resulted in an overall reduction of predation risk from this species, which is consistent with the recent reduction in Merlin occurrence at the study site (Buchanan 2009), but may not be consistent with overall greater effectiveness of two predator species.

In contrast to theory that predicts IG prey will not persist in highly productive environments occupied by IG predators (Holt and Polis 1997), and in support of empirical studies (Amarasekare 2008), my results suggest persistence of IG prey in the presence of IG predators at a site that supports a substantial abundance of Dunlins (Buchanan 1988a, Evenson and Buchanan 1997), a shared prey species. Various strategies are available to IG prey that would favor their coexistence with an IG predator: (a) temporal segregation, (b) distance-sensitive avoidance, and (c) habitat-mediated avoidance (Janssen et al. 2007, Sergio et al. 2007). Both falcon species

appear to hunt shorebirds throughout the mid- and low-tide period of exposed mudflats, suggesting that temporal segregation does not explain coexistence. Distance-sensitive avoidance is difficult to evaluate because the spatial distribution of the falcons is generally unknown except for the brief periods when they hunt. Although Merlins now typically use less of the estuary when hunting, their space use of the estuary has been subsumed in the area used by Peregrine Falcons, suggesting that distance-sensitive avoidance did not occur.

The final strategy, habitat-mediated avoidance, appears to have been adopted by Merlins at my study site. According to various interpretations of this strategy, the IG prey should either avoid habitats used by the IG predator, in which case the two predators would coexist in the same landscape, but use different habitats (Sergio et al. 2007), or the IG prey could use features of the habitat to reduce detection by, or as refuge from, the IG predator (Lima 1993, Janssen et al. 2007, Amarasekare 2008). In particular, the close proximity of capture locations to cover suggests that Merlins have altered their previous approach to hunting in favor of behavior that relies more on vigilance and stealth and involves prey capture close to the protective cover of vegetation. Such a strategy would allow them to effectively manage components of predation risk: rate of encounter, time spent vulnerable to encounters, and the probability of death given an encounter (Lima and Dill 1990). Peregrine Falcons sometimes use prominent perches in the uplands adjacent to the estuary (J. Buchanan unpubl. data), and a Merlin could monitor the larger falcon's presence while using the cover of upland vegetation to position itself for a brief attack at prey near shore and at a safe distance from the IG predator.

Predators may influence potential prey (including IG prey) at local or population scales (Lima 1998), and such effects can be distributed unevenly (Kauffman et al. 2007, Rayner et al. 2007). The recovery of Peregrine Falcons in western Washington appears to have influenced aspects of the occurrence and hunting behavior of Merlins at my study site. Although a relatively small estuary, this site supported a substantial number of Dunlins (Buchanan 1988a, Evenson and Buchanan 1997). Merlin abundance in western Washington has not declined since the recovery of Peregrine Falcon populations (Buchanan 2009), suggesting that mesopredator effects to date are site-specific and have not influenced Merlin abundance in the region. I hypothesize that mesopredator

suppression will vary according to local conditions, and should be most obvious at sites where shared prey is either abundant or preferred by the apex predator. Conversely, where Peregrine Falcons primarily target waterfowl, shorebirds are uncommon, or escape cover is optimal, Merlins may be less influenced by the presence of Peregrine Falcons because the degree of prey sharing is reduced (Holt and Polis 1997) and competitive or IGP effects are reduced. Additional work is required to further investigate aspects of the apex predator—mesopredator relationship that was the focus of my study, particularly to clarify temporal or spatial patterns of site use and to evaluate whether or how Merlins minimize competition and manage risk in the presence of Peregrine Falcons.

ACKNOWLEDGMENTS

With the exception of support from National Science Foundation grant SOS SPI-8004760 during January–March 1981, this project was independently funded. I thank Will Cresswell, R. Wayne Nelson, Fabrizio Sergio, Aaron Wirsing, Iñigo Zuberogoitia and an anonymous referee for providing comments that improved drafts of the manuscript.

LITERATURE CITED

- AMARASEKARE, P. 2008. Coexistence of intraguild predators and prey in resource-rich environments. *Ecology* 89: 2786–2797.
- ARIM, M. AND P.A. MARQUET. 2004. Intraguild predation: a widespread interaction related to species biology. *Ecology Letters* 7:557–564.
- BERGER, K.M., E.M. GESE, AND J. BERGER. 2008. Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology* 89:818–828.
- BRENNAN, L.A., J.B. BUCHANAN, S.G. HERMAN, AND T.M. JOHNSON. 1985. Interhabitat movements of wintering Dunlins in western Washington. *Murrelet* 66:11–16.
- BUCHANAN, J.B. 1988a. The abundance and migration of shorebirds at two Puget Sound estuaries. *Western Birds* 19:69–78.
- . 1988b. The effect of kleptoparasitic pressure on hunting behavior and performance of host Merlins. *Journal of Raptor Research* 22:63–64.
- . 1996. A comparison of Merlin and Peregrine Falcon hunting success in two coastal habitats. *Journal of Raptor Research* 30:93–98.
- . 2009. Changes in the winter occurrence of Merlins at a western Washington estuary following recovery of Peregrine Falcon populations. *Journal of Raptor Research* 43:149–151.
- , S.G. HERMAN, AND T.M. JOHNSON. 1986. Success rates of the Peregrine Falcon (*Falco peregrinus*) hunting Dunlin (*Calidris alpina*) during winter. *Raptor Research* 20:130–131.

- , C.T. SCHICK, L.A. BRENNAN, AND S.G. HERMAN. 1988. Merlin predation on wintering Dunlins: hunting success and Dunlin escape tactics. *Wilson Bulletin* 100: 108–118.
- CADE, T.J., J.H. ENDERSON, C.G. THELANDER, AND C.M. WHITE. [EDS.]. 1988. Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID U.S.A.
- CHAKAROV, N. AND O. KRÜGER. 2010. Mesopredator release by an emergent superpredator: a natural experiment of predation in a three level guild. *PlosOne* 5 (12): e15229. doi:10.1371/journal.pone.0015229.
- DEKKER, D. 1980. Hunting success rates, foraging habits, and prey selection of Peregrine Falcons migrating through central Alberta. *Canadian Field-Naturalist* 94:371–382.
- . 1988. Peregrine Falcon and Merlin predation on small shorebirds and passerines in Alberta. *Canadian Journal of Zoology* 66:925–928.
- . 2003. Peregrine Falcon predation on Dunlins and ducks, and kleptoparasitic interference from Bald Eagles wintering at Boundary Bay, British Columbia. *Journal of Raptor Research* 37:91–97.
- DURANT, S.M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal Ecology* 67:370–386.
- EVENSON, J.R. AND J.B. BUCHANAN. 1997. Seasonal abundance of shorebirds at Puget Sound estuaries. *Washington Birds* 6:34–62.
- GESE, E.M. AND S. GROTHE. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. *American Midland Naturalist* 133:36–43.
- HAKKARAINEN, H. AND E. KORPIMÄKI. 1996. Competitive and predatory interactions among raptors: an observational and experimental study. *Ecology* 77:1134–1142.
- HENKE, S.E. AND F.C. BRYANT. 1999. Effects of coyote removal on the faunal community in western Texas. *Journal of Wildlife Management* 63:1066–1081.
- HOLT, R.D. AND G.A. POLIS. 1997. A theoretical framework for intraguild predation. *American Naturalist* 149:745–764.
- JANSSEN, A., M.W. SABELIS, S. MAGALHÃES, M. MONTERRAT, AND T. VAN DER HAMMEN. 2007. Habitat structure affects intraguild predation. *Ecology* 88:2713–2719.
- KAUFFMAN, M.J., M. VARLEY, D.W. SMITH, D.R. STAHLER, D.R. MACNULTY, AND M.S. BOYCE. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters* 10:690–700.
- KIMBRELL, T., R.D. HOLT, AND P. LUNDBERG. 2007. The influence of vigilance on intraguild predation. *Journal of Theoretical Biology* 249:218–234.
- KOSTRZEWA, A. 1991. Interspecific interference competition in three European raptor species. *Ethology, Ecology and Evolution* 3:127–143.
- LIMA, S.L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bulletin* 105:1–47.
- . 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* 48:25–34.
- AND L.M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- ORIAN, G.H. 1969. Age and hunting success in the Brown Pelican (*Pelecanus occidentalis*). *Animal Behaviour* 17:316–319.
- PAGE, G. AND D.F. WHITACRE. 1975. Raptor predation on wintering shorebirds. *Condor* 77:73–83.
- PALMER, R.S. 1988. Handbook of North American birds, Vol. 5. Diurnal raptors. Yale Univ. Press, New Haven, CT U.S.A.
- PALOMARES, F. AND T.M. CARO. 1999. Interspecific killing among mammalian carnivores. *American Naturalist* 153:492–508.
- PECKARSKY, B.L., P.A. ABRAMS, D.I. BOLNICK, L.M. DILL, J.H. GRABOWSKI, B. LUTTBEG, J.L. ORROCK, S.D. PEACOR, E.L. PREISSER, O.J. SCHMITZ, AND G.C. TRUSSELL. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology* 89:2416–2425.
- PETTY, S.J., D.I.K. ANDERSON, M. DAVISON, B. LITTLE, T.N. SHERRATT, C.J. THOMAS, AND X. LAMBIN. 2003. The decline of Common Kestrels *Falco tinnunculus* in a forested area of northern England: the role of predation by Northern Goshawks *Accipiter gentilis*. *Ibis* 145:472–483.
- POLIS, G.A. AND R.D. HOLT. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution* 7:151–153.
- , G.A. MEYERS, AND R.D. HOLT. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297–330.
- PRUGH, L.R., C.J. STONER, C.W. EPPS, W.T. BEAN, W.J. RIPPLE, A.S. LALIBERTE, AND J.S. BRASHARES. 2009. The rise of the mesopredator. *BioScience* 59:779–791.
- RATCLIFFE, D. 1980. The Peregrine Falcon. Buteo Books, Vermillion, SD U.S.A.
- RAYNER, M.J., M.E. HAUBER, M.J. IMBER, R.K. STAMP, AND M.N. CLOUT. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Science* 104:20862–20865.
- SERGIO, F. AND F. HIRALDO. 2008. Intraguild predation in raptor assemblages: a review. *Ibis* 150(Supplement 1): 132–145.
- , L. MARCHESI, AND P. PEDRINI. 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *Journal of Animal Ecology* 72:232–245.
- , ———, ———, AND V. PENTERIANI. 2007. Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? *Animal Behaviour* 74:1607–1616.
- SOULÉ, M.E., D.T. BOLGER, A.C. ALBERTS, J. WRIGHT, M. SORICE, AND S. HILL. 1988. Reconstructed dynamics of rapid extinctions of chapparral-requiring birds in urban habitat islands. *Conservation Biology* 2:75–92.

- VANCE-CHALCRAFT, H.D., J.A. ROSENHEIM, J.R. VONESH, C.W. OSENBURG, AND A. SIH. 2007. The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology* 88:2689–2696.
- WARKENTIN, I.G., N.S. SODHI, R.H.M. ESPIE, A.F. POOLE, L.W. OLIPHANT, AND P.C. JAMES. 2005. Merlin (*Falco columbarius*). In A. Poole [Ed.], The birds of North America online, No. 44. Cornell Lab of Ornithology, Ithaca, NY U.S.A. <http://bna.birds.cornell.edu/bna/species/044>.
- WHITE, C.M., N.J. CLUM, T.J. CADE, AND W.G. HUNT. 2002. Peregrine Falcon (*Falco peregrinus*). In A. Poole and F. Gill [Eds.], The birds of North America, No. 660. The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC U.S.A.
- ZUBEROGOITIA, I., J.E. MARTÍNEZ, J. ZABALA, J.A. MARTÍNEZ, A. AZKONA, I. CASTILLO, AND S. HIDALGO. 2008. Social interactions between two owl species sometimes associated with intraguild predation. *Ardea* 96:109–113.
- AND M. PROMMER. 2011. The effect of intraguild predation on forest-dwelling raptors. Pages 168–175 in I. Zuberogoitia and J.E. Martínez [Eds.], Ecology and conservation of European forest-dwelling raptors. Diputación Foral de Bizkaia, Bilbao, Spain.
- ZUKERBERG, M. AND S. PEARSON. 2006. Kennedy Creek Natural Area Preserve management plan. Washington Dept. Natural Resources, Olympia, WA U.S.A.

Received 31 September 2011; accepted 21 March 2012
Associate Editor: Ian G. Warkentin