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PERSPECTIVE

Pinniped predation of birds: A cause for conservation concern?

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ABSTRACT

Recovering predators can create challenges for conservation objectives when they prey on vulnerable species. Although largely uncommon, pinniped predation of birds presents one such challenge. Here, we describe the novel characteristics of this predator–prey interaction, its impact on bird populations, and possible mitigation responses. We do so both broadly, synthesizing the wider literature, and specifically, in reference to ongoing South American sea lion (*Otaria flavescens*) predation of Black-necked Swans (*Cygnus melancoryphus*) we are currently observing in southern Chile. Our review of the literature suggests that in most cases bird predation by pinnipeds is only exhibited by a small proportion of the population, spreads socially between individuals, can be temporally severe, and may rapidly threaten the viability of bird populations. We discuss feasibility and efficacy of potential mitigation measures highlighting that, as foraging specializations can be socially transmitted, any such actions need to be time conscious as bird-killing behaviors may be increasingly difficult to remove. The contrasting population trends of pinnipeds and seabirds suggests that pinniped predation of vulnerable waterbirds is going to be an increasingly common conservation challenge in the future.

Keywords: bird predation, foraging specializations, human–wildlife conflict, pinnipeds, predator–prey interactions

Depredación de aves por Pinípedos: ¿una causa de preocupación para la conservación?

RESUMEN

La recuperación de depredadores puede generar desafíos para los objetivos de conservación cuando estos depredan especies vulnerables. Aunque poco común, la depredación de aves por pinnípedos representa uno de esos desafíos. En esta Perspectiva, describimos características novedosas de esta interacción depredador-presa y su impacto sobre poblaciones de aves antes de discutir qué debería hacerse para mitigar sus impactos, en caso de ser necesario. Esto lo hacemos en términos generales, sintetizando la literatura disponible, y específicamente, en referencia a la depredación de *Cygnus melancoryphus* por *Otaria flavescens* que estamos observando actualmente en el sur de Chile. Nosotros identificamos que la depredación de aves por pinnípedos es exhibida por una pequeña proporción de la población, se propaga socialmente entre individuos, puede ser temporalmente severa y puede amenazar rápidamente la viabilidad de poblaciones de aves. En este contexto, discutimos la viabilidad y eficacia de posibles medidas de mitigación, destacando que, dado que el comportamiento puede transmitirse socialmente, cualquier acción de este tipo debe considerar el tiempo, ya que estos comportamientos pueden ser cada vez más difíciles de eliminar. Las tendencias poblacionales contrastantes de pinnípedos y aves sugieren que la depredación por pinnípedos de poblaciones de aves será un desafío de conservación cada vez más común en el futuro.

Palabras clave: conflicto humano-vida silvestre, depredación de aves, especializaciones de alimentación, interacciones depredador-presa, pinnípedos

INTRODUCTION

Conservation efforts have resulted in some impressive recoveries of once depleted populations of large-bodied predators (Magera et al. 2013, Cruz et al. 2019). This is important as these animals are critical components of ecosystems (Ritchie and Johnson 2009) and also have intrinsic value in their own right. Yet, while predator resurgences are to be celebrated, they can also present significant new challenges in wildlife management, especially if they have top-down effects on species of conservation concern (Marshall et al. 2016). For example, the (human-assisted) recovery of Bald Eagles (*Haliaeetus leucocephalus*) in Voyageurs National Park, USA, has apparently come at the expense of other recovering piscivorous bird species (Cruz et al. 2019).

Pinnipeds (sea lions, fur seals, true seals, and the walrus) provide another interesting case in point. In recent decades many pinniped populations have increased dramatically after being heavily depleted by commercial harvesting and culling programs (Bowen and Lidgard 2013, Magera et al. 2013). These are generalist, opportunistic predators that can compete for prey that have economic or conservation value to humans. Yet, while much attention has been paid to their interactions with fisheries and aquaculture (e.g., Sepúlveda et al. 2015), pinniped predation of birds presents a novel, interesting, and occasionally urgent, conservation challenge.

One such challenge is currently playing out in the Río Cruces wetland, a Ramsar Site and Nature Sanctuary located in Valdivia, southern Chile (39.74°S, 73.25°W), where, in July 2018, monthly Black-necked Swan (*Cygnus melancoryphus*) surveys (conducted since 1987 by Corporación Nacional Forestal, CONAF; Jaramillo et al. 2018) began recording predation of swans by South American sea lions (*Otaria flavescens*). While initially ascribed to a single sub-adult male, other individuals were soon sighted exhibiting the same predatory behavior. The sea lions were pulling swans under the water before consuming part of the carcass, most often just the pectoral muscle (Figure 1). Swan hunting, handling, and (partial) consumption was fast, and individual sea lions were observed catching and killing as many as 5 adult birds in the space of 25 min (E. Jaramillo personal observation). Overall predation, judged by the number of carcasses, increased rapidly to 133 swans in a single month and, although predation subsided during the sea lion's breeding period (when the animals return to their coastal rookeries; Baylis et al. 2017), recent carcass counts suggest it is still increasing.

Although Black-necked Swans are not internationally threatened (BirdLife International 2016), the Rio Cruces wetland and surrounding habitat is the species' most important breeding site and the swans are considered a priority in the sanctuary's management objectives (Jaramillo et al. 2018, CONAF 2019a). Indeed, the wetland's current population (estimated at ~13,000 individuals in the 2018 breeding season; CONAF 2019b) has only recently recovered from a 2004 collapse that followed a pollution event (Jaramillo et al. 2018). Therefore, despite monitoring that suggests a continued positive population trend (CONAF 2019b), there are concerns that increased predation by sea lions might threaten this population.

Socially, swans are important to people in Valdivia; their conservation was a central motivator in one of Chile's most significant environmental conflicts after the 2004 collapse (Sepúlveda and Villarroel 2012). As a result, swan predation by sea lions has attracted much media attention and debate (e.g., Villalobos 2018). Indeed, the issue has created a management conundrum for Chilean authorities where all options, including doing nothing, are contentious. This is partly a consequence of the novelty of this particular predator–prey interaction; there is little specific scientific evidence to indicate how best to proceed. In this context we searched the literature for journal articles and reports that shed light on the ecology or management of pinniped predation of birds. We used the Google Scholar and Web of Knowledge databases between August and November 2019 to find relevant material (published in the last 30 yr) using all combinations of 5 key terms (predation or bird predation or mitigation or management or interaction) with the 5 terms for species within the clade Pinnipedia (pinniped or sea lion or fur seal or seal or walrus). Additional studies

FIGURE 1. Predation of a Black-necked Swan (*Cygnus melancoryphus*) by a South American sea lion (*Otaria flavescens*) in the Río Cruces wetland, Valdivia, Chile (**A**), and the carcass of a depredated swan (**B**). Photographs by F. Dreves and F. Navarro, respectively.

were located by searching the reference lists of relevant material from the initial search.

CHARACTERIZING PINNIPED PREDATION OF BIRDS

We found instances of bird predation by pinnipeds from across the world involving a diverse range of avifauna such as penguins (Charbonnier et al. 2010, Ryan and Kerr 2012, Morrison et al. 2017), cormorants (Marks et al. 1997, Johnson et al. 2006), gannets (Makhado et al. 2006, 2013), albatrosses (Moore et al. 2008), auks (Mallory et al. 2004), and ducks (Tallman and Sullivan 2004, Lovvorn et al. 2010). Many of these interactions share similar characteristics and we identify 4 traits that appear to characterize pinniped–bird predation.

Bird Predation is only Exhibited by a Small Proportion of the Pinniped Population

With the exception of the leopard seal (*Hydrurga leptonyx*; Hall-Aspland and Rogers 2004) and possibly some populations of Antarctic fur seals (*Arctocephalus gazelle*; Casaux et al. 2004), birds form a negligible part of pinniped diet at a population level (Kirkman 2009). Instead, bird predation appears to be an uncommon foraging specialization that, when exhibited, is only conducted by certain individuals within the population. Indeed, even within these animals, there may be marked variation in prey handling behavior (du Toit et al. 2004). Males, and specifically sub-adult males, are the most common culprits (David et al. 2003, du Toit et al. 2004, Makhado et al. 2009; although see Lalas et al. 2007).

Foraging Specializations can be Socially Transmitted within Pinniped Populations

Several studies report that, at their sites, pinniped predation of birds is a relatively new and increasing phenomenon (Charbonnier et al. 2010, Voorbergen et al. 2012). A number of non–mutually exclusive hypotheses have been posed to explain this behavior including the depletion of "regular" prey, increased pinniped–bird interactions, an extension of play behavior, and the general reduction in pinniped culling as a management strategy (du Toit et al. 2004, Kirkman 2009). There is also speculation that, once a foraging specialization is displayed by one animal in a population, it can be learned by others (Makhado et al. 2006). Observations of established bird predators interacting with other "new" bird predators during hunts provides provisional support for this hypothesis (Marks et al. 1997). The strongest evidence of pinnipeds learning novel foraging behaviors from conspecifics, however, comes from research by Schakner et al. (2016) who applied a network-based diffusion analysis to show how learned behaviors, in this case learning to utilize a dam to depredate fish, spread within populations. These results appear to confirm that, although bird predation may involve only a limited number of individuals when it is first recorded, it may quickly spread to others (Marks et al. 1997, Makhado et al. 2006). Interestingly, bird predation still appears to be dominated by sub-adult males even when the behavior becomes more established in a population (David et al. 2003).

Bird Predation by Pinnipeds can be Temporally Severe

While some birds appear to recognize the threat that pinnipeds present and respond appropriately (Charbonnier et al. 2010, Lovvorn et al. 2010), others make easy prey. Johnson et al. (2006) observed Cape fur seal (*Arctocephalus pusillus*) predation of African Penguins (*Spheniscus demersus*) and cormorants (*Phalacrocorax* sp.) and report just a single unsuccessful attempt in 204 initiated hunts. Such success rates are consistent with the naïve prey hypothesis where birds (1) fail to recognize the threat that pinnipeds present, (2) have inappropriate antipredator responses, and/or (3) their responses are appropriate but ineffective (Banks and Dickman 2007). Indeed, the recognition of pinnipeds as predators appears not to be innate for some bird species (Marks et al. 1997, du Toit et al. 2004). As a result, a single pinniped can kill many individual birds in a short space of time. For instance, an Atlantic walrus (*Odobenus rosmarus*) was recorded to have hunted and consumed 67 Thick-billed Murre (*Uria lomvia*) in one day (Mallory et al. 2004), while a lone New Zealand sea lion (*Phocarctos hookeri*) was able to depredate 128 adult Royal Albatross (*Diomedea epomophora*; one of the largest flying birds in the world), in just a few weeks (Moore et al. 2008). Although the population-level effects of walrus on murres is unknown (Mallory et al. 2004), the number of albatrosses killed by the sea lion represented "a large and ongoing effect" on the albatross population (Moore et al. 2008). In these and other instances, the consumption of only a small proportion of the bird carcass (if any) may serve to elevate predation rates (du Toit et al. 2004, Moore et al. 2008, Ryan and Kerr 2012).

Most reported examples of severe, sustained predation come from the vicinity of bird breeding colonies (Kirkman 2009). Plausible explanations include high densities of prey making the behavior profitable (Ainley et al. 2005), predictable spatial use making adult birds more vulnerable (Lalas et al. 2007), and/or the presence of naïve juvenile birds (David et al. 2003). It is also possible that there is reporting bias within the literature as the area around colonies is easiest to observe (Makhado et al. 2006), and ad hoc reports document birds being opportunistically depredated away from breeding sites (e.g., Tallman and Sullivan 2004).

Pinniped Predation can Threaten the Viability of Bird Populations

The literature contains examples of, apparently, one-off incidents of bird predation that are not suggestive of any wider, population-level, impacts (e.g., Mallory et al. 2004, Tallman and Sullivan 2004). However, there is clear evidence that, when continued, pinniped predation can be unsustainable; imperiling both sub-populations and species (Lalas et al. 2007, Voorbergen et al. 2012, Makhado et al. 2013, Weller et al. 2016, Morrison et al. 2017). Predation by a limited number of New Zealand sea lion (in this unusual incidence, females) has been identified as a key threat to the viability of a small population of endangered Yellow-eyed Penguin (*Megayptes antipodes*; Lalas et al. 2007). Pinniped predation threatens not only small isolated populations of birds. For example, predation by Cape fur seal of small numbers of Cape Gannet (*Morus capensis*) around Malgas Island, South Africa (the second largest Cape Gannet colony in the world), was first recorded in the late 1980s, and an estimated 1.2–2.5% of fledglings were killed in 1989–1990. This percentage increased to 30% in 2000–2001, then above 50% in 2005–2006 (reviewed in Makhado et al. 2006). Losses during this latter period were as high as 10,800 birds per annum, reducing the colony by 25% in just 5 yr (Makhado et al. 2006). Cape Gannets have recently been reclassified as "Endangered" on the IUCN Red List with fur seal predation identified as a key threat (BirdLife International 2018).

WHAT, IF ANYTHING, SHOULD BE DONE?

Pinnipeds are intelligent, generalist predators and optimal foraging theory predicts that they (1) will target easily caught prey with quick handling times and (2) consume only those parts that yield the highest calorific return (Sih 1980). Indeed, there are examples of pinniped species developing similarly noteworthy foraging specializations on cetaceans (Leopold et al. 2015), fish (Schakner et al. 2016), and even other pinnipeds (Womble and Conlon 2010). Yet, as we have seen, the rapid top-down impacts on the bird populations can be severe. Such cases may prompt wildlife practitioners to consider if mitigation is feasible and appropriate.

The most common direct action applied to reduce pinniped predation of birds appears to be the killing of "bird-specialist" individuals (David et al. 2003, du Toit et al. 2004, Moore et al. 2008, Makhado et al. 2009). Reviews of marine mammal culling and "problem individual" removal can be found elsewhere (see Bowen and Lidgard 2013 and Swan et al. 2017, respectively), but this strategy merits some specific discussion. From an ecological perspective, there is evidence that, where bird predation is limited to a small number of animals, their prompt removal can entirely remove the problem (Moore et al. 2008). Where the behavior is established in a pinniped population, selective culling may reduce bird mortality rates (David et al. 2003, du Toit et al. 2004, Makhado et al. 2009, Weller et al. 2016). However, the chance of stopping bird predation altogether appears to decline with the number of animals that display such behavior (Schakner et al. 2016), especially if individuals learn to avoid humans (Makhado et al. 2009). In these instances, benefits are likely to be temporary, requiring ongoing selective removal (Makhado et al. 2006, Schakner et al. 2016). Here, culling may be most effective if concentrated at specific sites (Weller et al. 2016) and in time periods when birds are most vulnerable (e.g., post-fledging; Makhado et al. 2009). From a conservation perspective, it should also be noted that, as many of the pinniped species being discussed (e.g., fur seals and sea lions) are strongly polygynous, the removal of a small number of sub-adult males is unlikely to influence population reproductive rates (Lalas et al. 2007, Moore et al. 2008). Socially, killing animals, even for conservation purposes, requires ethical considerations and is likely to be contentious (especially in Chile; Villatoro et al. 2019).

Envisaging a strong social response to pinniped killing, what are the nonlethal options available to address heavy bird predation? Acoustic harassment devices have shown promise in deterring pinniped predation in river systems (Yurk and Trites 2000) and at fish farms (Götz and Janik 2015). However, these devices require predation to be spatially concentrated and so are unlikely to be effective in many pinniped–bird interactions. Aversive conditioning or "hazing" (attempting to change an animal's behavior through associations with a negative impact) has also been trialed to reduce pinniped predation of salmonids, albeit with disappointing results: the animals learned to avoid the negative stimulus and it did not reduce predation (Brown et al. 2008). It is possible that "problem individuals" could be removed from the area. Some have suggested taking habitual bird predators into captivity (Lalas et al. 2007). Such a step would require sites with the appropriate infrastructure and resources to care for these animals indefinitely (Brown et al. 2008). The translocation of animals is a nonlethal method that commonly has high social acceptability but also high financial cost (Fontúrbel and Simonetti 2011). However, if the correct animal could be captured alive (mortality of pinnipeds can be high during live capture: Brown et al. 2008), pinnipeds can navigate in unfamiliar waters and research on fur seals (*Arctocephalus* spp.) in Tasmania suggests that the majority would return within a short time period (Robinson et al. 2008). Finally, managers can also choose to do nothing. Whether this alternative is effective or not will depend on the characteristics of the predation event. Furthermore, if the affected species is charismatic (as with the Valdivian swans), this alternative may not be socially acceptable. In summary, although nonlethal methods exist, there is little evidence to suggest they would be an effective means of mitigating severe pinniped predation of birds.

Despite this synthesis, we are split as to the correct management avenue in respect to the ongoing Black-necked Swan predation in Valdivia—a situation not uncommon in the management of charismatic fauna. Although we have the advantage of regular census data and carcass counts, other basic ecological information, such as immigration and mortality rates, is still missing. Some of us judge that the risk of the behavior spreading, and predation continuing to increase, justifies the lethal removal of "problem" sea lions. Others consider that, as the conservation threat to swans is currently minimal and there is evidence that the swan population is increasing despite sea lion predation (CONAF 2019b), any lethal measures taken to protect the swans may set an unwelcome precedent in native predator management. This is a particular concern in Chile where there is growing social conflict over pinniped interactions with fisheries and aquaculture, and there have been requests for more active interventions (Sepúlveda et al. 2015). Despite our differences, we all agree that any decision, including "do nothing," needs to be well justified.

FUTURE DIRECTIONS

Broad trends of monitored seabirds indicate a 70% decline between 1950 and 2010 (Paleczny et al. 2015) as a consequence of anthropogenic causes such as commercial fisheries, pollution, and invasive species (Croxall et al. 2012). This is in stark contrast to the fortunes of pinnipeds where 50% of populations are considered "significantly increasing" (Magera et al. 2013). Although severe pinniped predation of birds is uncommon, we suggest that, given these trends, such interactions will likely increase. We also highlight the "predator-pit" scenario, where bird populations that have been reduced or fragmented as a result of anthropogenic activities will have lower resilience to respond to the pressure of pinniped predation (e.g., Lalas et al. 2007, Weller et al. 2016).

There is certainly plenty of scope for research into the ecology of this predator–prey interaction. For those wishing to inform management decisions, we outline 6 key questions and research approaches (Table 1). Detailed, site-specific investigations should be complemented by broader analyses that explore the variables that might make bird populations vulnerable to pinnipeds (e.g., abundance of alternative prey, breeding density, distance to pinniped breeding site). Indeed, despite much speculation (Kirkman 2009), little scientific attention has been paid to the underlying ecological drivers that produce these situations. Such analyses would allow an improved assessment of future risk.

In the meantime, we recommend monitoring for predation in those areas where threatened, fragmented, or important bird populations are found in close proximity to pinniped populations—especially fur seals and sea lions. This would not only catch this behavior in its early stages, but would provide valuable data to inform management (Table 1). Indeed, because methods to mitigate pinniped predation have ecological and social consequences that require thorough assessment, wildlife practitioners may also want to proactively evaluate potential actions. Structured decision-making provides a framework to navigate "tough multidimensional choices characterised by uncertain science, diverse stakeholders, and difficult trade-offs" (Gregory et al. 2012). It does so by providing a framework to (1) identify management objectives, (2) promote transparency in decisions, (3) include multiple stakeholders, (4) develop predictions, and,

TABLE 1. Key research and management questions for locations where pinniped predation of birds is a conservation concern.

	Key questions	Research approach	Example
1	Is bird predation present?	Monitoring with regular observational surveys	CONAF 2019b
2	Are predation rates increasing?	Quantifying predation via observations of predation/ carcasses or scat analysis	Makhado et al. 2006
3	Does predation threaten population viability?	A population viability analysis using predation rates, population sizes/ growth rate	Lalas et al. 2007
4	Is the behavior being socially transmitted?	Network-based diffusion analysis using sight–resight data on individual pinnipeds during haul-outs and predation	Schakner et al. 2016
5	What effect would pinniped management have on predation?	Epidemiological (susceptible–infected) models can assess selective culling when behavior is socially transmitted or system dynamic modelling can be applied to consider efficacy of removal when managing multiple threats	Schakner et al. 2016, Weller et al. 2016
6	Will management achieve social and ecological objectives?	Structured decision-making framework that establishes utility thresholds (e.g., minimum bird productivity) corresponding to conservation objectives	Martin et al. 2010

ultimately, (5) identify optimal decisions for management objectives (Martin et al. 2010, Gregory et al. 2012). As such, the approach has been successfully applied to conserve bird populations under threat due to predation by native predators (Martin et al. 2010).

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