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CONSERVATION LETTER: EFFECTS OF GLOBAL CLIMATE CHANGE ON RAPTORS[1]

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INTRODUCTION

Global climate change is an ongoing pervasive global conservation concern, with significant negative impacts for many species and populations. This Conservation Letter provides a scientific review of the effects of global climate change on raptors and concludes by highlighting potential mitigations and research needs. This letter is not intended as an exhaustive literature review. Rather, the intent of the Raptor Research Foundation (RRF) is to provide readers with enough evidence-based examples that they can appreciate the scope and prevalence of climate change impacts, understand their effects on raptor species and populations, and recognize some of the challenges associated with addressing climate change's effects on raptors across regions.

Climate change is caused by the release of atmospheric greenhouse gases (primarily carbon dioxide) resulting in changes in global climate-related parameters, mainly temperature and precipitation. In this scenario, the trend of increasing global temperatures is predicted to continue (Intergovernmental Panel on Climate Change [IPCC] 2021), influencing other climatic parameters and events. Increasing temperatures can impact raptors directly (e.g., Jaffré et al 2013, Dykstra et al. 2021b) and indirectly by driving disruptions to water cycles ranging from more frequent heavy precipitation events (Trenberth et al. 2003, Min et al. 2011, Anctil et al. 2014) to more severe drought (Cook et al. 2018, Smith et al. 2020). Further, the nature of climate events is also changing, encompassing more severe hurricanes and tropical cyclones (Emanuel 2005, 2013, Holland and Bruyère 2014), a poleward expansion of tropical cyclones (Studholme et al. 2022), and shifts in precipitation temporal trends (Dunning et al. 2018), exposing raptors to stochastic events. Climatic changes also alter the distributions of primary producers (Sturm et al. 2001, Tape et al. 2006) creating bottom-up effects that alter ecosystem function (i.e., "regime shifts"; Rodionov 2004, Ripple et al. 2014). Moreover, the risk of wildlife extinctions is substantially accelerated by climate change (Urban 2015), and climate warming is related to the recent extinctions of at least one raptor (Sergio et al. 2021). This suggests there may be major negative effects of climate change for raptors (McClure et al 2018).

Raptors are valuable and important study systems for investigating the effects of climate change because raptors are widespread, perform important ecological functions and can serve as flagship species for biodiversity (Donázar et al. 2016). As long-lived top predators holding large home ranges and preying on a wide variety of vertebrates and invertebrates, raptors are influenced by the effects of environmental change on lower trophic levels (Meserve et al. 2003, Schmidt et al. 2018) and can serve as biotic multipliers of climate change (Urban et al. 2017). Raptors have been the focus of multiple long-running studies on

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migration (e.g., Sullivan et al. 2016, Therrien et al. 2017) and breeding rate (e.g., Fasce et al. 2011, Jiménez-Franco et al. 2020, Maciorowski et al. 2021), which provide valuable long-term data sets that allow assessment of change (e.g., Lee et al. 2020). Additionally, raptors with specialized habitat or feeding strategies are likely to be disproportionally affected by climate change because of their narrow ecological niche and lack of plasticity (Gilg et al. 2012, Hof et al. 2012). Understanding the threats posed by climate change and identifying priority areas and species is critical for raptor conservation.

Effects of Climate Change on Raptors

Climate change affects raptors in various ways, including changes to distributional ranges, disease and parasite ecology, breeding phenology, migration, abundance, population dynamics, communities, and morphology, physiology, and behavior (Møller 2013, Dunn and Møller 2019). We here provide a brief overview of some of these effects on raptor species and raptor populations.

Distributional Range. A raptor's geographic range is governed largely by the overlap between the spatial distribution of their thermal niche, preferred prey species, and appropriate nesting substrate. In response to changing climate, species could alter their physiological tolerance via evolutionary processes, but given the rapid pace of climate change and mobility of raptors, range shifts that track their thermal niches are likely to predominate (Gilg et al. 2012). Range shifts are well documented in a variety of taxa (e.g., Parmesan et al. 1999, Vors and Boyce 2009, Zuckerberg et al. 2009, Huang et al. 2017), including raptors (Paprocki et al. 2014, McCaslin and Heath 2020), and at different time frames (Parmesan 2006, Tingley et al. 2009, Saupe et al. 2019). The predominant trend for range shift is poleward and increased elevation, but the direction and magnitude of range shifts can vary by species, life history, dietary habits, and habitat, with notable differences between wintering and breeding ranges (see Migration section below; Reside et al. 2010, Hovick et al. 2016, Curley et al. 2020), although many raptors display a propensity for northward shifts (Paprocki et al. 2014, McCaslin and Heath 2020). Tropical raptors are a notable exception to this trend because their range is predicted to shift multidirectionally (Sutton et al. 2020, 2022), tracking fluctuations in precipitation (rather than temperature); precipitation being the primary driver of reproductive success in this region (Pearce-Higgins and Green 2014).

Raptor range shifts are likely to facilitate changes to ecosystem structure with important consequences for conservation. Novel assemblages created by shifting ranges may alter ecosystem functions (top-down regulation of prey and competition for resources) with consequences that are difficult to predict because of the many variables and interactions involved (Gilman et al. 2010). Altered community dynamics are likely to disproportionally impact specialist (Hof et al. 2012, Lurgi et al. 2012) and range-restricted species (particularly polar and mountain-top species) because of range contractions (e.g., the tundra biome may contract up to 34% [Boonman et al. 2022]). For example, Peregrine Falcons (*Falco peregrinus*) preferentially select warmer habitats within Nunavut, Canada (Peck et al. 2018) likely due to higher survival and recruitment (Bruggeman et al. 2015). It is reasonable to expect the range of Peregrine Falcons to shift northward resulting in increased competitive pressure on the more specialized Gyrfalcon (see Population Dynamics section). Defining current and future raptor ranges is useful to assess the effectiveness of priority or protected areas (Paprocki et al. 2014, Kassara et al. 2017) and to contextualize population parameters, as traditional monitoring efforts (within a stationary study area) are typically unable to differentiate emigration from population declines (Viverette et al. 1996, Paprocki et al. 2015). Further, shifts in thermal niches should be considered within the context of life history and other critical habitat requirements (e.g., prey and nesting substrate), because temperature alone is insufficient to accurately predict range shifts.

Diseases and Parasites. Climatic change is also facilitating the mostly northward movement of diseases, parasites, and ectoparasites (McFadzen et al. 1996, Bradley et al. 2005, Hemert et al. 2014), disrupting host-pathogen dynamics (Merino 2019) and changing local disease ecology. Greater cross-species viral transmission and infection of naive populations can result from disease range expansions and the development of novel assemblages (Kafle et al. 2020, Carlson et al. 2022). This can have drastic implications for naïve populations (e.g., populations responding to avian malaria [*Plasmodium* spp.]; Atkinson and Lapointe 2009) because virulence varies based on a species' historical exposure to the disease (Lapointe et al. 2012, Ings and Denk 2022), as examplified by the Gyrfalcon's greater sensitiveity to malaria compared to the Peregrine Falcon (Kingston et al. 1976). Similiarly, novel ecoparasites (e.g., poultry bugs [*Haematosiphon inodorus*]) can elicit significant negative effects on raptors including decreased nestling body condition and survival (Dudek et al. 2021), aid in vector-mediated disease transmission (Leighton et al. 2012), and facilitate indirect effects of weather changes (Lamarre et al. 2018). Further, prey can transmit diseases to raptors (Dudek et al. 2018); thus changes in diet composition can facilitate the transmission of novel pathogens to predators. Under environmental change, raptors can switch from primarily resident prey species to migratory prey (Heath et al. 2021), which may be problematic because migratory species serve as important reservoirs for diseases (e.g., avian influenza) and provide a conduit for disease to travel vast distances to span seemingly disconnected systems (Seekings et al. 2021, Tanikawa et al. 2021). Lastly, novel diseases and parasites can impact lower trophic levels and elicit bottom-up effects for raptor populations. Changing disease ecology as a result of climate change is a central conservation concern for raptors and likely provides the strongest probability of direct effects, including increased mortality and rapid population declines.

Breeding Phenology. Many bird species exhibit earlier annual breeding dates (advanced phenology) as a result of climate change, and that shift influences diet and reproductive rate (Dunn 2019, Dunn and Møller 2019). Advanced breeding phenology may have positive effects on reproduction, as early breeders often produce more young (Franks et al. 2018). Conversely, if a bird species fails to advance its breeding phenology, there may be a temporal mismatch between the species' nestling rearing period and the peak abundance of its primary prey. The mismatch could potentially lead to lower survival of young (Dunn 2019) and other demographic and evolutionary changes (Miller-Rushing et al. 2010, Visser and Gienapp 2019) that can have important conservation implications.

Species in several groups of raptors are exhibiting advancing phenology, including falcons (Steenhof and Peterson 2009, Burnham and Burnham 2011, Carrière and Matthews 2013, Smith et al. 2017, Taylor et al. 2021, Callery et al. 2022a), accipiters (Lehikoinen et al. 2010, Rosenfield et al. 2017), buteos (Lehikoinen et al. 2009, Terraube et al. 2014), and others (Sergio 2003, Moreno-Rueda et al. 2019). Yet an approximately equal number of studies found no trend, and a few found delayed breeding, including some of the same species studied in different locations, and several species of owls (see compiled table in Dykstra et al. 2021a, Supplementary Material Table S1 for more information; also Lehikoinen et al. 2013, Callery et al. 2022a).

Whether a raptor species advances its breeding phenology may be influenced by dietary preferences and trophic level (Dunn and Møller 2014, Dunn 2019). Many species with advancing trends consume primarily birds or insects, whereas those lacking trends are mostly generalists or mammal-specialists (Dykstra et al. 2021a). This suggests that ornithophagous raptors may track the shifting hatching dates of their avian prey, which themselves may be tracking insect hatching, promoting a better match of peak food availability to nestlings' energy requirements (Bretagnolle and Terraube 2019). However, one study revealed advancement of three trophic levels (oak trees, caterpillars, and passerines) but a lack of response by the secondary consumer (Eurasian Sparrowhawk [*Accipiter nisus*]), which specializes on juvenile songbird species that hatch sequentially, providing an extended period of available prey (Both et al. 2009). Overall, it is unclear how diet influences a raptor's ability to adapt to climate change. A recent review concluded that generalist predators were no more buffered from the effects of climate change than were specialists (Bretagnolle and Terraube 2019), but more research is needed.

Raptors nesting at high latitudes, where effects of global climate change are more significant (Bekryaev et al. 2010), more often exhibit advanced phenology, compared to raptors in more temperate regions. Peregrine Falcons nesting in the Arctic advanced their phenology (Carrière and Matthews 2013) whereas those in Spain did not (Zuberogoitia et al. 2018). Mammal-specialist buteos breeding at high latitudes also shifted their breeding dates (Lehikoinen et al. 2009, Terraube et al. 2014). The advancing breeding dates of high-latitude raptors are likely driven by the shorter window of breeding opportunity compared to their temperate counterparts, or possibly intra-species competition; hence, high-latitude species have a greater incentive (and less room for error) to track advancing temperature to ensure breeding success.

Among a variety of avian species, advancing egg-laying dates are associated with larger clutch sizes (Dunn and Møller 2014) and greater reproductive success (McLean et al. 2016, Dunn 2019). However, evidence is limited for raptors, and the relationship between advancing phenology and reproduction apparently varies among species and locations. In several species, no trends in reproductive rates were documented despite advanced phenology (Sergio 2003, Lehikoinen et al. 2009, Steenhof and Peterson 2009, Rosenfield et al. 2017, Taylor et al. 2021). However, advanced phenology was linked to larger clutch sizes in Montagu's Harriers (*Circus pygargus*; Moreno-Rueda et al. 2019), but decreased reproductive success in Rough-legged Hawks (*Buteo lagopus*; Terraube et al. 2014). Among American Kestrels (*Falco sparverius*) nesting in the western USA, breeding dates advanced and early nesters experienced both greater reproductive success and higher adult survival. Conversely, in an eastern population, breeding dates showed no trend and early nesters had greater reproductive success but lower adult survival, suggesting that a trade-off between reproduction and survival may limit eastern kestrels' ability to adjust their breeding dates (Callery et al. 2022a). Thus, the influence of phenology change on reproduction is apparently variable or limited for raptors, though data are sparse.

Migration. The long-term, standardized study of raptor migration has provided valuable databases to investigate migration phenology and raptor abundance (Sullivan et al. 2016, Therrien et al. 2017). Overall, raptors have delayed their autumn migration (Therrien et al. 2017) and simultaneously advanced their spring migration (Sullivan et al. 2016); however, parsing the data by migration strategy reveals important differences between short-distance and long-distance (trans-equatorial) migrants. In eastern North America, short-distance migrants delayed their autumn departure, whereas long-distance migrants did not (Therrien et al. 2017); yet long-distance migrants in the same study areas advanced their spring migration the most (Sullivan et al. 2016). Similarly, European short-distance migrants both delayed their autumn migration and advanced their spring migration with warmer climate conditions (Jaffré et al. 2013). At one watch site in the Pyrenees in France, some short-distance migrants delayed, but most long-distance migrants advanced their autumn migration dates (Filippi-Codaccioni et al. 2010). Delayed autumn migration is the likely cause of delayed arrival to the wintering grounds (Harris et al. 2013), but this is understudied.

Migratory short-stopping (i.e., making a shorter autumn migration, resulting in a wintering range nearer to the breeding range) has been documented for many raptor species (Goodrich et al. 2012, Heath et al. 2012, Martín et al. 2014, 2019, Morrison and Baird 2016, Condro et al. 2022). Some partial migrants are less likely to migrate than they were in past decades (e.g., Common Kestrel [*Falco tinnunculus*], Holte et al. 2016; Eurasian Buzzard [*Buteo buteo*], Holte et al. 2017; Red-tailed Hawk [*Buteo jamaicensis*], Paprocki et al. 2017). Further, short-distance migrants appear more predisposed to shift their range compared to long-distance migrants (Hovick et al. 2016, McCaslin and Heath 2020), potentially driven by a greater ability to respond to supplemental cues, which could encourage resident behavior in partially migratory populations (Paprocki et al. 2017).

Migratory behavior is influenced by environmental conditions, and changes in raptor migration vary according to the extent of environmental change and the migration strategy of the species. Arctic-nesting raptors progressively follow snowmelt as they migrate north in spring, though the degree of their responsiveness to snowmelt differs (Curk et al. 2020). Movements of Rough-legged Hawks were closely associated with snowmelt across the landscape and this species tended to be at places where snow cover was moderate and melting was at its peak (Curk et al. 2020). Snowy Owls (*Bubo scandiacus*) migrated just ahead of the north-moving progression of snowmelt whereas Peregrine Falcons migrated just behind it (Curk et al. 2020). Snow cover delays spring arrival dates of American Kestrels throughout their range (Powers et al. 2021) and decreases the availability of small mammals (Naughton 2012); both snowmelt patterns and prey availability may be expected to change with global climate change. Species with flexible or irruptive migration strategies such as the Snowy Owl and Rough-legged Hawk will likely adjust more easily to changing conditions than those with more regular migration such as the Peregrine Falcon (Curk et al. 2020). For species with variable migration strategies, short-distance migrants are more likely to adjust to temperature variation than are long-distance migrants (Powers et al. 2021).

Changes in wind patterns and atmospheric conditions attributable to global climate change can potentially reduce the suitability of traditional migration routes (Nourani and Yamaguchi 2017, Nourani et al. 2017), resulting in changing migratory behaviors. Soaring raptors are particularly sensitive to conditions that influence thermals (Duerr et al 2015); for example, diminished thermal updrafts or increased precipitation can compel Turkey Vultures (*Cathartes aura*) to make stopovers and keep them from resuming migration (Mallon et al. 2021).

Extreme weather events also influence migratory behavior. An increase in the number of hurricanes and large storms might be expected to influence raptor migration strategies and success, though this is understudied. For example, global weather conditions (as indexed by the North Atlantic Oscillation [NAO]) during autumnal migration were correlated with survival of Arctic-breeding Peregrine Falcons; positive NAOs, which indicated conditions likely to spawn hurricanes, were associated with greater survival. Researchers attributed this unexpected result to the stronger Northeast Trade Winds associated with positive NAOs, which may have made it easier for the falcons to cross the Gulf of Mexico on their southward journey (Franke et al. 2011).

Populations. *Abundance.* Raptors, like other birds, exhibit changes in abundance and/or density as a consequence of gradual environmental change (shifts in precipitation regime, rising temperatures) or extreme weather events (major hurricanes, severe drought) associated with climate change. Both modeling and empirical studies demonstrate variable responses of raptor abundance to climate change, with endangered, endemic, and range-restricted species being the most vulnerable to such changes.

Abundance models for endangered raptor species suggest climate change may cause important population declines. Niche modeling for the endangered Sokoke Scops-Owl (*Otus ireneae*) predicts decreasing abundance of owls and their range area (Monadjem et al. 2013) with higher CO_2 emissions. Similarly, simulated precipitation changes (i.e., decreased mean annual precipitation and increased interannual variation) predict dramatic reductions of Tawny Eagle (*Aquila rapax*) populations in African savannas (Wichmann et al. 2003). Empirical studies demonstrate that extreme weather events mostly affect bird populations indirectly via habitat destruction (Wunderle et al. 1992). Raptor populations show variable responses to extreme weather events, although most decline in abundance. Declines were observed in 25% of raptor populations after a major hurricane (Wauer and Wunderle 1992), and the abundance of specific species (Ferruginous Pygmy-Owl [*Glaucidium brasilianum*], Grenada Hook-billed Kite [*Chondrohierax uncinatus mirus*]) declined significantly after hurricane disturbance (Lynch 1991, Thorstrom and McQueen 2008). In contrast, numbers of open-area raptors (American Kestrel, Roadside Hawk [*Rupornis magnirostris*]) remained unchanged after hurricane disturbance (Lynch 1991, Wauer and Wunderle 1992), as did the mean number of territorial pairs of Mediterranean raptors after storms with heavy snowfall, extremely low temperatures, and winds with steady speeds >100 km/hr (Martínez et al. 2013). Raptors' abundance can decrease or increase in response to climate change, but more research is needed to elucidate patterns of response among different raptor species or groups (tropical, temperate, specialist, generalist).

Changes in abundance of raptors among habitat types following extreme weather events suggest between-habitat movement after disturbance. The abundance of Turkey Vultures and Black Vultures (*Coragyps atratus*) increased with greater cover of wetlands in areas affected by a major hurricane (Martínez-Ruiz et al. 2021). Moreover, vulture abundance was higher in the first months following hurricane landfall; such responses were likely explained by the rapid resource pulse in habitats like wetlands (Martínez-Ruiz et al. 2021), which can ameliorate the effects of disturbance for some species. Unfortunately, few studies have examined effects of other extreme events (e.g., floods) on raptors, which may impact raptor species differently (Hruska 2016).

Population dynamics. Climate change influences raptor population dynamics directly through precipitation or temperature reducing raptor productivity and survival, or indirectly through altered prey population dynamics (including changing herbivore cycles [Ims et al. 2008, Kausrud et al. 2008, Cornulier et al. 2013]). Mechanisms can include destabilizing pressures that affect population fluctuations, alter wavelengths, or halt cycles entirely. Gilg et al. (2009) and Schmidt et al. (2012) found a climate-change-induced collapse in collared lemming (*Dicrostonyx groenlandicus*) cycles caused a concurrent collapse of Snowy Owl population cycles. This led to a 98% reduction in owl productivity and local extirpations. Similarly, climate-change-induced dampening of vole cycles substantially reduced the breeding probability of Tawny Owls (*Strix aluco*) and may drive the local population in the United Kingdom to extirpation (Millon et al. 2014). Though direct effects of weather on mortality rates may be easier to document, effects of altered predator-prey dynamics are typically considered more consequential (Millon et al. 2014, Ockendon et al. 2014, Terraube et al. 2014).

Extreme weather events and changing weather patterns can dramatically alter population dynamics of raptors (and their prey). In Greenland, an extreme weather event (high snowfall and late snowmelt) led to an ecosystem-wide reproductive collapse in an area previously characterized by decades of regular lemming-based predator-prey population cycles (Schmidt et al. 2018). Precipitation events negatively impacted productivity of Arctic Peregrine Falcons in Canada (Anctil et al. 2014, Robinson et al. 2017, Lamarre et al. 2018) and Arctic-nesting Rough-legged Hawks (Pokrovsky et al. 2012). Similar effects, including reduced adult survival, have also been documented at more temperate locations (McDonald et al. 2004, Fisher et al. 2015). Sarasola et al. (2005) reported direct mortality of individuals of six raptor species, as well as 14 other raptors with severe injuries, after a single hailstorm in central Argentina. Following major hurricanes, the endangered Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*) population decreased from 75 to 19 individuals (75% decrease) according to post-hurricane counts (McClure et al. 2023). At lower latitudes, extreme heat events also cause direct mortality; Catry et al. (2011) found nestling mortality increased substantially during anomalous heat events and predicted that climate-change-induced extreme heat could reduce the Lesser Kestrel (*Falco naumanni*) population size by as much as 7% annually. Mass mortality associated with extreme weather events may have direct consequences on the local abundance of raptors (Sarasola et al. 2005), and direct mortality can have broader negative effects for endangered populations (e.g., Puerto Rican Sharp-shinned Hawk). Reduced precipitation in arid regions can negatively impact raptor population dynamics by reducing the probability of population persistence (Wichmann et al. 2003). Higher precipitation levels or changing average temperatures during the breeding season (as predicted in current and future climate scenarios) have been correlated with lower raptor productivity (Mearns and Newton 1988, Bradley et al. 1997, Lehikoinen et al. 2009), with the potential to influence raptors' demographics over longer periods of time.

Raptor Communities. There is scarce information on raptor-community responses to climate change, but available evidence shows species-specific reductions leading to community changes, reductions in community parameters, and among-habitat movements reflecting shifting precipitation regimes and extreme weather events. Raptor density was significantly lower in tropical dry forests impacted by a major hurricane compared to unaffected nearby forests (Martínez-Ruiz and Renton 2018). Concurrently, species richness and evenness were significantly higher in wetlands located within the area of maximum hurricane winds, suggesting raptor species' movement among habitats and use of wetlands as refugia after hurricane disturbance (Martínez-Ruiz and Renton 2018). The occupancy probability for Accipitridae and Falconidae declined significantly more than that of other bird families in response to a long-term reduction in precipitation attributable to climate change in the Mojave Desert (Iknayan and Beissinger 2018); individual raptor species (American Kestrel, Prairie Falcon [*Falco mexicanus*], Turkey Vulture, Sharp-shinned Hawk [*Accipiter striatus*]) showed significant declines in occupancy, causing decreases in species richness of the overall bird community (Iknayan and Beissinger 2018). Similarly, species richness of avian scavengers and occasional scavengers (including Bald Eagle [*Haliaeetus leucocephalus*], Barred Owl [*Strix varia*], Black Vulture, Cooper's Hawk [*Accipiter cooperii*], Golden Eagle [*Aquila chrysaetos*], Great Horned Owl [*Bubo virginianus*], Red-shouldered Hawk [*Buteo lineatus*], Red-tailed Hawk, Rough-legged Hawk, and Turkey Vulture) is predicted to decrease up to 80% over the next 50 yr, as a response to the predicted warmer climate for the eastern USA (Marneweck et al. 2021).

Shifts in the rainfall regime can influence raptor communities via shifts in prey abundance occurring after heavy rainfall in arid systems. In Australia, raptor richness increased after extreme rainfall events and an associated rodent-irruption, with increases mainly driven by increases in generalist raptors (Pavey and Nano 2013). Variation in system productivity of arid systems as a result of climate change may strongly influence raptors, as raptor richness increases with productivity of land, but decreases with the proportion of deserts in arid-system assemblages (Anadón et al. 2010). Other raptor communities may respond differently to changes in primary productivity, and effects may be influenced by community composition.

Although evidence of raptor community responses to climate change is still limited, we can expect increases in species richness, indirectly favored by resource pulses and prey irruption associated with some extreme events (e.g., higher precipitation), as well as reductions in species richness in arid systems warming because of climate change. The magnitude of effects of climate change in raptor communities across the globe will also depend on the available pool of regional species, a concern in some areas where raptor communities have been described as depauperate.

Morphology, Physiology, and Behavior. Changing conditions can promote rapid change in morphological and physiological traits via phenotypic plasticity or microevolutionary processes (Millien et al. 2006, Karell et al. 2011, del Mar Delgado et al. 2019). Phenotypic plasticity more commonly facilitates a response to climate change, although distinguishing between plasticity and microevolution is difficult and understudied (Teplitsky and Charmantier 2019).

Generally decreasing body sizes have been documented across multiple avian taxa (Yom-Tov and Yom-Tov 2006, Van Buskirk et al. 2010, Gardner et al. 2014, Tornberg et al. 2014 McKechnie 2019) but causes have not been confirmed. Decreasing body size has been proposed as a third "universal" response to climate change (together with distributional and phenological shifts; Gardner et al. 2011), although recent reviews show more inconsistent trends (Teplitsky and Millien 2014, Fiedler 2021). Migrating American Kestrels declined in size and mass at most but not all of seven North American sites, concurrent with declining abundance of migrating kestrels; thus, the smaller size may be attributable to lower food availability, climate change, or other factors (Ely et al. 2018). An inverse relationship between body size and temperature aligns with Bergmann's rule, though the specific mechanisms promoting this rule are debated (Gardner et al. 2014, Brammer and Humphries 2015).

For polymorphic species, climate change can influence the proportion of the color morphs in a population through selective pressure on this highly heritable trait. For example, survival of brown morph Tawny Owls in Finland is inversely related to snow depth, but as mean snow depth declined over time as a consequence of climate change, selection pressure eased and survival improved. As a result, brown morphs composed an increasing proportion of the population over the study period (Karell et al. 2011).

Physiological and behavioral mechanisms for coping with heat are relatively plastic; thus, large impacts of climate change may be expected where species are already near their physiological limits, such as in deserts with high environmental temperatures and limited water supply (Iknayan and Beissinger 2018, McKechnie 2019). Acute consequences — hyperthermia and dehydration — can occur quickly, especially in small species (McKechnie 2019). Heat and drought can also generate longer-term consequences including chronic mass loss, which can be attributed to heat-dissipating behaviors (e.g., panting; du Plessis et al. 2012) or indirect effects on the prey base (Cruz-McDonnell and Wolf 2016). Temperature extremes can reduce nestling growth and survival rates (Cunningham et al. 2013, Cruz-McDonnell and Wolf 2016, McKechnie 2019), which may have carryover effects on population dynamics. For example, body mass declines of adult and nestling Burrowing Owls (*Athene cunicularia*), along with delayed breeding, reduced reproductive rate, and declining population, were linked to drought conditions in arid New Mexico (Cruz-McDonnell and Wolf 2016). Raptors may be more vulnerable to climate change than smaller bird species in the Mojave Desert, though their declines were more likely related to lower prey availability than to direct physiological constraints (Iknayan and Beissinger 2018).

Raptor behavior may also change in response to the pressures of global climate change. For example, late-nesting kestrel males begin incubation sooner after nest initiation, which advances the hatch date of the first eggs, reducing the amount of phenological mismatch. The resulting increased asynchrony of the brood also helps reduce peak energetic demands (Callery et al. 2022b). Overall, the effects of global climate change on raptor morphology, physiology and behavior have received limited study and warrant further attention.

RESEARCH NEEDS AND FUTURE DIRECTIONS

Raptors have been and will continue to be affected by the environmental pressures of climate change, resulting in changes in their phenologies and dynamics. Given the predicted acceleration of climate change (IPCC 2021), some raptor species will become more vulnerable to the higher variation in climate conditions and more extreme weather patterns.

Identifying populations or species most likely to be severely affected by climate change is critically important, as is designing actions that can maintain and increase resilience of these species. High-altitude raptors and those in hot arid zones are likely at greater risk because of the severity and rate of local climate change. Species with low population sizes or inherent limiting factors (e.g., island species, dietary specialists), and those facing anthropogenic threats (e.g., habitat loss, persecution) might also be particularly vulnerable to the compounding effects of environmental pressures. It is probable that the effects of climate change on many raptors are still unknown because of a lack of basic biological and ecological information on some species, including tropical raptors. We must continue assessing which species are at higher risk and how high priority species will respond spatially to climate change to adequately inform conservation actions and management of vulnerable species (Moritz and Agudo 2013).

Predicting future distributional shifts is useful for species conservation, as is monitoring populations' shifting distributions and/or changing phenologies. As with other birds, this information should be used for designing effective conservation strategies, identifying potential conflicts with human developments (Marini et al. 2009), and identifying priority areas for protection that preserve biodiversity under predicted distributional changes (Virkkala et al. 2014). Importantly, recent shifts in migration behavior, phenology of migration, flight paths, and weather patterns might affect detectability and timing of raptors passing migration-monitoring sites, and we need to be able to incorporate such changes within the framework of migration monitoring. We recommend sharing data on this topic among researchers (e.g., via repositories) and taking the time to curate long term data; these actions will promote a better understanding of raptor responses to global climate change and support the development of a well-founded framework of potential actions to conserve raptors worldwide.

Novel interactions as a result of distributional changes may have greater implications for specialist raptors interacting with a new assemblage of species, pathogens, or anthropogenic threats, or intra-guild competitors with similar niches (Oliver and Morecroft 2014). It is important to consider such interactions involving raptors in both their breeding and nonbreeding ranges, if these differ. Monitoring projects that involve trapping raptors should incorporate the collection of samples for examination of pathogens and disease to better track such threats for raptor species and populations. There is also an urgent need for better models incorporating climate change into predictive models of population dynamics (Sæther et al. 2019) and ecological niche models (Zurell and Engler 2019) for raptors. Additionally, all species-specific and community-level studies should be prioritized to elucidate causal mechanisms that influence raptors under the climate change scenario.

Existing long-term breeding phenology datasets should be analyzed to assess trends across a wider variety of raptors. A raptor-specific meta-analysis would give insight into patterns and a better understanding of which species and populations are most vulnerable. Such an analysis could also improve predictions of how trends in breeding phenology influence reproduction and other population parameters. Because long-term datasets often rely on older data derived from "low-tech" methods (e.g., banding/ringing, citizen-science breeding season and nonbreeding season counting, migration counts), these efforts should be continued to maintain the continuity and usefulness of the data into the future (Ambrosini et al. 2019). However, these need to be combined with more modern research methods.

Studies on the effects of single extreme weather events on raptors are still scarce, but the available evidence of direct mortality and significant population reduction of endangered raptors indicates that more attention should be directed to this topic. In addition, there is little information on the effects of other extreme weather events such as severe wildfires (e.g., Australia's wildfire season of 2020), which cause mortality of different animals, but evidence is still scarce for raptors.

As more extreme weather events are expected with climate change, it is important to evaluate how different raptor species (and populations and communities) cope with such events, and to identify species-specific traits (diet, size, nest type, phenology) that are associated with species' resilience. Additionally, identifying the most vulnerable populations located at sites that are expected to be severely affected by extreme weather events will help prioritize management efforts (restoring of vegetation, refugia [Sumasgutner et al. 2020]) to mitigate the direct impacts of weather.

Some effects of climate change may be partially mitigated by conservation efforts that provide critical resources for raptors. Provision of nest boxes for some species such as Peregrine Falcons can buffer the negative effects of weather variables including extreme weather events (Sumasgutner et al. 2020). Similarly, provision of artificial water sources in desert zones may help species minimize dehydration risk exacerbated by higher temperatures, though care should be taken in the siting of such resources, and it is unclear how they might affect predation risk for species visiting them (McKechnie et al. 2019). Overall, monitoring, assessing data, and mitigation actions may not be enough for the maintenance of raptor populations; these actions must be accompanied by global actions to reduce climate change.

As a leading professional society for raptor researchers and raptor conservationists, the RRF is dedicated to the accumulation and dissemination of scientific information about raptors, and to resolving raptor conservation concerns (RRF 2021). Effects of climate change on raptors are of conservation concern, presenting a global threat to raptor populations. Based on the science summarized here, we conclude that a world-wide reduction in carbon emissions is necessary to allow long-term co-existence of raptors with human populations, but that some conservation efforts can help mitigate the effects of climate change on raptors.

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