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CANNIBALISM IN RAPTORS: A REVIEW

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ABSTRACT.—Feeding strategies, including cannibalism (in which an individual eats a member of the same species), are an important aspect of predator ecology. Cannibalism comprises five forms in raptors: siblicide, filicide, non-parental infanticide, conspecific strife, and conspecific scavenging. Cannibalism by raptors has been documented opportunistically for over a century, but it is unknown how frequent or widespread the behavior is. We performed the first systematic literature review and meta-analyses of the studies documenting filicide, non-parental infanticide, conspecific strife, and conspecific scavenging by raptors. We found 29 reports of these types of cannibalism; we did not review reports of siblicide due to the high frequency of the behavior, making it nearly ubiquitous among raptors. Filicide had nearly twice as many reports ($n = 11$, 37.9%) as any other type of cannibalism. Most reports were direct observations ($n = 23$, 79.3%), and nearly half the reports came from North America ($n = 14$, 48.3%) and approximately a third from Europe ($n = 10$, 34.5%). The 29 reports involved 25 raptor species from four families, with those from Acciptridae most common ($n = 19$, 65.5%). Cannibalism in raptors varies but most involves nestlings, which are easier to kill than adults, possibly because brood reduction can help the stronger young survive. Documented reports of cannibalism are increasing, possibly due to recent technological advancements that have increased our ability to document cannibalism and other ecological processes. Nevertheless, we encourage future reports of cannibalism from under-represented locations and for taxa that are less well-studied.

KEY WORDS: *camera trap; cannibalism; competition; diet; filicide; infanticide; scavenging; siblicide.*

CANNIBALISMO EN RAPACES: UNA REVISIÓN

RESUMEN.—Estrategias de alimentación, incluyendo el canibalismo (en el cual un individuo come un miembro de su misma especie), son un aspecto importante de la ecología de la depredación. El canibalismo incluye cinco formas en las rapaces: fratricidio, filicidio, infanticidio no parental, lucha entre individuos conspecíficos y consumo de carroña de individuos conspecíficos. El canibalismo por parte de las rapaces ha sido documentado de modo oportunista desde hace más de un siglo, pero se desconoce cómo de frecuente o generalizado es este comportamiento. Realizamos la primera revisión sistemática de la literatura y un meta-análisis de los estudios que documentaron filicidio, infanticidio no parental, lucha entre

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individuos conespecíficos y consumo de carroña de individuos conespecíficos por rapaces. Encontramos 29 informes de estos tipos de canibalismo; no revisamos los informes de fratricidio debido a la alta frecuencia de este comportamiento, haciéndolo casi ubicuo entre las rapaces. El filicidio apareció en casi el doble de informes ($n = 11$, 37.9%) que cualquier otro tipo de canibalismo. La mayoría de los informes fueron observaciones directas ($n = 23$, 79.3%), y cerca de la mitad de los informes vinieron de Norteamérica ($n = 14$, 48.3%) y aproximadamente un tercio de Europa ($n = 10$, 34.5%). Los 29 informes involucraron 25 especies de rapaces incluidas en cuatro familias, siendo los Acciptridae los más comunes ($n = 19$, 65.5%). El canibalismo en rapaces varía, pero la mayoría involucra polluelos, que son más fáciles de matar que los adultos, posiblemente porque la reducción de la nidada puede ayudar a la supervivencia de los jóvenes más fuertes. Los informes que documentan el canibalismo van en aumento, posiblemente debido a avances tecnológicos recientes que han aumentado nuestra capacidad para documentar el canibalismo y otros procesos ecológicos. Sin embargo, alentamos la realización de futuros estudios de canibalismo provenientes de lugares subrepresentados y para taxones que son menos estudiados.

[Traducción del equipo editorial]

INTRODUCTION

Feeding strategies and prey selection are central to ecology, especially for predators. Prey choice dictates the ecological niches and habitats selected by predators, and to a large extent their reproductive success and survival (Newton 1998, 2010). Most vertebrate predators scavenge or steal food on occasion (Sebastian-Gonzales 2019, Inagaki et al. 2020). Cannibalism is a less common strategy for food acquisition in which an individual consumes a conspecific. Cannibalism occurs throughout the animal kingdom, and is often a means of increasing fitness and survival by improving nutrition while also reducing competition (Markham and Watts 2007, Hadjikyriakou and Kirschel 2016). Consuming a competitor provides nutrition and reduces competition for food (e.g., killing a sibling in a nest also reduces immediate competition for food brought by parents).

Cannibalism may take one of five forms: siblicide, filicide, non-parental infanticide, conspecific strife, and conspecific scavenging. Siblicide is the killing and eating of siblings in the nest, and is a form of competition linked to brood reduction (Bechard 1983, Redondo et al. 2019). Filicide is the killing of nestlings by parents who then eat the nestling or feed it to other nestlings; usually it is nestlings that are unlikely to survive that are killed (Bortolotti et al. 1991). Non-parental infanticide is conspecific killing and eating of young animals still dependent on their parents. In birds, this type of predation is most common at nests (Hadjikyriakou and Kirschel 2016). Conspecific strife, in which birds aggressively fight and occasionally kill their adult competitors, can also lead to cannibalism if the winner of the contest eats the competitor it killed (de Lecea et al. 2011). Scavenging is behavior in which animals consume

carion (e.g., Wilson and Wolkovich 2011), sometimes via kleptoparasitism in which an individual actively steals procured food (e.g., Holthuijze et al. 1987, Negro 1992). In this report, we limit our treatment of scavenging behavior to conspecific scavenging (i.e., cannibalism); one example of this is the scavenging of dead nestlings by their parents or siblings (Miller et al. 2015).

Raptors are predatory birds that specialize in the capture of mobile prey. Among raptors, siblicide is so common that it is nearly ubiquitous (Ingram 1959, Bechard 1983), and has been documented at least once in most families of raptors: Cathartidae (e.g., Margalida et al. 2004), Acciptridae (e.g., Pilz and Seibert 1978, Bortolotti et al. 1991), Tytonidae (e.g., Lenton 1984), Strigidae (e.g., Ingram 1962, Anderson 2015), and Pandionidae (e.g., Forbes 1991), but not in Sagittariidae. In comparison, filicide, non-parental infanticide, conspecific strife, and conspecific scavenging are much less reported.

We opportunistically documented scavenging activity on the carcass of a Red-tailed Hawk (*Buteo jamaicensis*) killed by a vehicle collision. We placed the carcass in a hedgerow on 11 January 2019 in Champaign County, Illinois, USA (40°07'N, 88°09'W), and monitored the carcass with a camera trap (Bushnell NatureView HD, Lenexa, KS, USA). On 23 January at 12:43 H we recorded an incident of a conspecific scavenging (Fig. 1), an event that prompted our investigation of cannibalism. To our knowledge there has never been a systematic review to determine how common cannibalism behaviors are in raptors.

METHODS

Literature Review. We performed a systematic literature review and meta-analysis of the scientific



Figure 1. Red-tailed Hawk exhibits conspecific scavenging in an Illinois hedgerow on 23 January 2019.

literature to understand the frequency and pattern of four types of cannibalism (filicide, non-parental infanticide, conspecific strife, and conspecific scavenging) in raptors. (We excluded siblicide because it is so common.) On 12 May 2019 we performed a systematic literature search using Web of Science for the cannibalism terms combined with the common and genus names for the orders Cathartiformes, Accipitriformes, and Strigiformes as listed in Clements et al. (2018). We removed publications not documenting cannibalism in raptors, publications not from peer-reviewed journals, and studies of domesticated raptors, and augmented our systematic review of the literature by searching the references of papers that we reviewed (e.g., snowball sampling). For each report, we considered meteorological seasons (Trenberth 1983), corresponding to spring (March to May), summer (June to August), fall (September to November) and winter (November to February) for the northern hemisphere and the opposite for the southern hemisphere. We also recorded whether the raptor observed was nesting at the time the cannibalism occurred, as reported by the author. We documented the frequency, type, and geographic extent of cannibalism, as indicated in the published reports.

RESULTS

We reviewed reports that documented one of four types of cannibalism (Table 1). Filicide had nearly twice as many reports ($n = 11$, 37.9%) as the other types of cannibalism we reviewed ($n = 6$ for each; Table 1). Cannibalism occurred during each of the four seasons, but most occurred during the species'

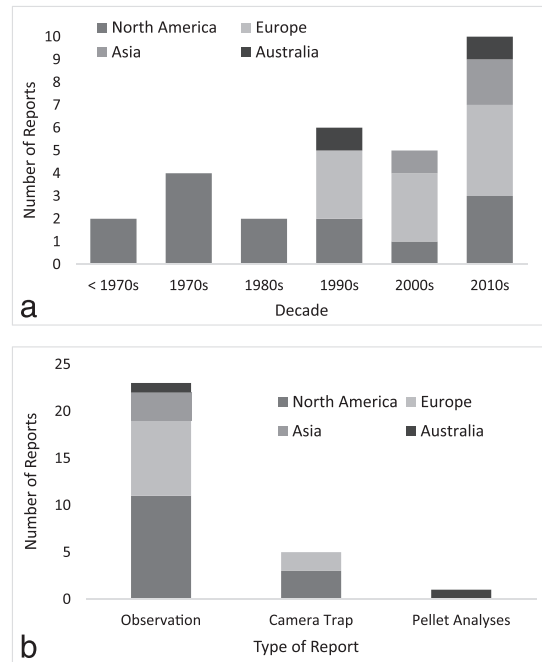


Figure 2. Frequency of reports of cannibalism by raptors represented by continent for (a) each decade and (b) type of report.

nesting season ($n = 18$, 64.3%; Table 1). The 29 reports involved 25 raptor species from four families. Raptors from Acciptridae were most common ($n = 19$, 65.5%), followed by Strigidae ($n = 5$, 17.2%), Cathartidae ($n = 4$, 13.8%), and Tytonidae ($n = 1$, 3.5%), but we found no reports for Sagittariidae or Pandionidae (Table 1). Among the genera in Acciptridae, the majority of reports concerned either *Falco* spp. ($n = 7$, 36.8%) or *Buteo* spp. ($n = 5$, 26.3%). Among raptor species, only Red-tailed Hawks ($n = 4$, 13.8%) and Eleonora's Falcon (*Falco eleonora*; $n = 2$, 6.9%) had multiple reports.

There has been a general increase in reports of cannibalism over time (Fig. 2a). The 2010s had the most reports ($n = 10$, 34.5%), followed by the 1990s ($n = 6$, 20.7%) and 2000s ($n = 5$, 17.2%). Most reports were direct observations ($n = 23$, 79.3%), with a few observations from camera traps ($n = 5$, 17.2%), and one record derived from pellet analyses (3.5%; Fig. 2b). Nearly half of the observations of cannibalism occurred in North America ($n = 14$, 48.3%) and approximately a third in Europe ($n = 10$, 34.5%). There were also reports from Asia ($n = 3$, 10.3%) and Australia ($n = 2$, 6.9%), but none from

Table 1. Literature review of cannibalism by raptors, including the raptor family and species, location, study type, season (*indicates nesting season), and type of cannibalism.

| STUDY | RAPTOR FAMILY | RAPTOR SPECIES | LOCATION | STUDY TYPE | SEASON | CANNIBALISM TYPE |
|---------------------------------|---------------|--|----------------------|-----------------|---------------|--------------------------|
| Steffen 1977 | Acciptridae | Red-tailed Hawk (<i>Buteo jamaicensis</i>) | Wisconsin, USA | Observation | Summer* | Conspecific Strife |
| Coffin 1906 | Acciptridae | Red-tailed Hawk (<i>Buteo jamaicensis</i>) | Indiana, USA | Observation | Not Reported | Conspecific Strife |
| Clevenger and Roest 1974 | Acciptridae | Red-tailed Hawk (<i>Buteo jamaicensis</i>) | California, USA | Observation | Winter | Conspecific Strife |
| Kang 2018 | Cathartidae | Cinereous Vulture (<i>Aegypius monachus</i>) | South Korea | Observation | Winter | Conspecific Strife |
| de Lecea et al. 2007 | Cathartidae | Griffin Vulture (<i>Gyps fulvus</i>) | Spain | Observation | Winter | Conspecific Strife |
| Fisher 1975 | Strigidae | Great Gray Owl (<i>Strix nebulosa</i>) | Alberta, Canada | Observation | Winter | Conspecific Strife |
| Bortolli et al. 1991 | Acciptridae | American Kestrel (<i>Falco sparverius</i>) | Saskatchewan, Canada | Observation | Summer* | Filicide |
| Caro et al. 2014 | Acciptridae | Bonelli's Eagle (<i>Aquila fasciata</i>) | Spain | Observation | Spring* | Filicide |
| Lyons and Mosher 1982 | Acciptridae | Broad-winged Hawk (<i>Buteo platypterus</i>) | Maryland, USA | Observation | Summer* | Filicide |
| Korman and Macek 2011 | Acciptridae | Golden Eagle (<i>Aquila chrysaetos</i>) | Slovakia | Observation | Spring* | Filicide |
| Temple 2008 | Acciptridae | Merlin (<i>Falco columbarius</i>) | England | Observation | Not Reported* | Filicide |
| Lewis 2017 | Acciptridae | Northern Goshawk (<i>Accipiter gentilis</i>) | Alaska, USA | Camera Trap | Summer* | Filicide |
| Frankie et al. 2013 | Acciptridae | Peregrine Falcon (<i>Falco peregrinus</i>) | Nunavut, Canada | Camera Trap | Summer* | Filicide |
| Hollhuijzen 1987 | Acciptridae | Prairie Falcon (<i>Falco mexicanus</i>) | Idaho, USA | Observation | Not Reported* | Filicide |
| Hollingsworth 2017 | Strigidae | Powerful Owl (<i>Ninox strenua</i>) | Victoria, Australia | Observation | Spring* | Filicide |
| Webster et al. 1999 | Strigidae | Powerful Owl (<i>Ninox strenua</i>) | Australia | Pellet Analyses | Not Reported* | Filicide |
| Sheffield 1994 | Tyrtonidae | Barn Owl (<i>Tyto alba</i>) | Texas, USA | Observation | Winter* | Filicide |
| Markham and Watts 2007 | Acciptridae | Bald Eagle (<i>Haliaeetus leucocephalus</i>) | Virginia, USA | Observation | Spring* | Non-parental Infanticide |
| Jones and Manez 1990 | Acciptridae | Black Kite (<i>Mitrus migrans</i>) | Spain | Observation | Summer* | Non-parental Infanticide |
| Hadjikyriakou and Kirschel 2016 | Acciptridae | Eleonora's Falcon (<i>Falco eleonorae</i>) | Cyprus | Camera Trap | Autumn* | Non-parental Infanticide |
| Steen et al. 2016 | Acciptridae | Eleonora's Falcon (<i>Falco eleonorae</i>) | Greece | Camera Trap | Autumn* | Non-parental Infanticide |
| Negro et al. 1992 | Acciptridae | Lesser Kestrel (<i>Falco naumanni</i>) | Spain | Observation | Not Reported* | Non-parental Infanticide |
| Arroyo 1997 | Acciptridae | Montagu's Harrier (<i>Circus pygargus</i>) | Spain | Observation | Summer* | Non-parental Infanticide |
| Mori 2017 | Acciptridae | Greater Spotted Eagle (<i>Clanga clanga</i>) | Gujarat, India | Observation | Autumn | Scavenging |
| <i>This Study</i> | Acciptridae | Red-tailed Hawk (<i>Buteo jamaicensis</i>) | Illinois, USA | Camera Trap | Winter | Scavenging |
| Camina and Palomo 2003 | Cathartidae | Eurasian Griffon Vulture (<i>Gyps fulvus</i>) | Spain | Observation | Winter | Scavenging |
| Rana and Prakash 2001 | Cathartidae | White-backed Vulture (<i>Gyps bengalensis</i>) | Rajasthan, India | Observation | Spring | Scavenging |
| Robinson 1954 | Strigidae | Burrowing Owl (<i>Athene cunicularia</i>) | Kansas, USA | Observation | Spring | Scavenging |
| Millard et al. 1978 | Strigidae | Great Horned Owl (<i>Bubo virginianus</i>) | Idaho, USA | Observation | Winter | Scavenging |

Africa, Antarctica, or South America (Fig. 2). In North America, most of the studies took place in the USA ($n = 11$, 78.6%) and the rest in Canada (Table 1). In Europe, most of the studies came from Spain ($n = 6$, 60%), with no other country having more than one report (Table 1).

DISCUSSION

Our literature review of cannibalism in raptors showed that cannibalism takes multiple forms with different evolutionary drivers. Most raptor cannibalism involves nestlings at the nest, the life stage during which raptors are the most vulnerable. Reports of siblicide during the nestling phase are so prevalent in the literature that it is likely nearly ubiquitous among raptor species. After siblicide, filicide was the most common type of cannibalism. There were also as many reports of non-parental infanticide as there were of conspecific strife or conspecific scavenging. Brood reduction via cannibalism (siblicide or filicide) can contribute to the success of a nest, with stronger young surviving (Bechard 1983), and appears to be an important evolutionary motivation for cannibalism by raptors.

Most reports of cannibalism were from Acciptridae species (65.5%), including every report of non-parental infanticide, 72.7% of the reports of filicide, and half of the reports of conspecific strife. We expect this is due to both the abundance of members of the Acciptridae and to the fact that many species occur in urban areas. Red-tailed Hawks were the species with the most reports of cannibalism, likely due to their large geographic range and abundance, although three reports were of conspecific strife. Reports of conspecific scavenging were evenly split with two reports each for Acciptridae, Cathartidae, and Strigidae. Reports of non-parental infanticide were most common among falcons, which are bird-hunters and sometimes nest at high densities in colonial or semi-colonial situations that may provide the opportunity for falcons to actively hunt the young in other nests.

The relative scarcity of studies in previous decades may also have been due to a lack of attention by researchers. All reports prior to the 1990s occurred in North America, with reports from Europe increasing after that. Other continents have few reports, but we doubt this is due to a lack of cannibalism by raptors in these areas but rather a lack of interest in publishing these reports by researchers. For example, observations of cannibalism by raptors in Africa are available through social

media, but have not made their way into peer-reviewed literature. We also note that some published observations of cannibalism are reported incidentally in the text of a larger paper on another topic (e.g., Red-shouldered Hawks (*Buteo lineatus*) cannibalizing their dead nestlings; [Woodford et al. 2008, Miller et al. 2015]; and these reports were not found using our literature review protocol. We hope this review increases interest in reporting observations of cannibalism, and we encourage reports from under-represented locations, and for taxa that are less well known, and of the more uncommon behaviors.

Although nest observations are a key study method in ornithology, recent technological advancements such as camera traps have increased our ability to document scavenging and other ecological processes (Krofel 2011, Allen et al. 2019, Inagaki et al. 2020). These techniques may increase documentation of cannibalism by raptors, but cannibalism may also be rarely observed because it is intrinsically rare due to the possible costs of the behavior (e.g., contracting parasitic infection or disease). Cannibalism by raptors seems to occur when they are energetically stressed; for example, most incidents occurred during the nesting season when the parents are providing food for young, and young are easily killed. One might expect that there would be selective pressure against conspecific scavenging unless the benefits of the food resource outweighed the risks of contracting a disease or parasite. Future research should focus on the fitness benefits of cannibalism, and other fundamental reasons it occurs. An experimental approach could also be used to determine the frequency of conspecific scavenging and cannibalism behavior, possibly by placing carcasses of different raptor species and other animals in the territory of a variety of raptors.

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