

OCCURRENCE AND EVOLUTION OF COOPERATIVE BREEDING AMONG THE DIURNAL RAPTORS (ACCIPITRIDAE AND FALCONIDAE)

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ABSTRACT.—Cooperative breeding, in which more than two individuals live in a group and raise offspring, usually in a single nest, is found in only 3% of avian species. On the basis of a review of the literature, we found reports of groups (usually trios) at nest sites in 42 species of diurnal raptors. At least one example of cooperative breeding was found in 29% of genera and 14% of species, distributed in both Accipitridae and Falconidae. Given the difficulty of obtaining behavioral observations necessary to detect cooperative breeding in most raptor species, combined with the large number of species that have been poorly studied, cooperative breeding in diurnal raptors may be more common than our data indicate. However, when data on the sex of the extra bird(s) or relationships among group members were available, patterns were quite varied. For 7 of 13 species, groups primarily contained multiple adult males, though three of those species also had groups formed from offspring that had delayed dispersal; three species had a low, but regular, occurrence of multiple females (females of groups laid eggs in the same nest); and the remaining three species were characterized by having extra birds that were yearlings or subadults. In over half of species, groups did not appear to be composed of related individuals, contrary to many cooperatively breeding passerine species where groups are primarily composed of offspring that have delayed dispersal. Our review suggests that the evolution of group living in many raptors may be independent of delayed dispersal, and that the factors important in explaining the evolution of that behavior depend upon the benefits of group living. *Received 7 January 2002, accepted 14 December 2002.*

RESUMEN.—La cría cooperativa, en que más de dos individuos viven en un grupo y crían prole (generalmente en un solo nido), se observa en sólo el 3 % de las especies de aves. Con base en una revisión bibliográfica, encontramos reportes de grupos (tríos en su mayoría) en los nidos de 42 especies de rapaces diurnas. Al menos un ejemplo de cría cooperativa se encontró en el 29 % de los géneros y el 14 % de las especies, tanto en Accipitridae como en Falconidae. Dada la dificultad de obtener las observaciones etológicas necesarias para detectar cría cooperativa en la mayoría de las aves de presa, además del gran número de especies que no ha sido estudiado, pudiera ser que este fenómeno fuese más común de lo que sugiere nuestro estudio. Sin embargo, cuando se tuvo información sobre el sexo de las aves excedentes o sobre el parentesco entre los miembros del grupo, se detectaron una variedad de patrones. En 7 de las 13 especies, los grupos estuvieron conformados por machos adultos; 3 de esas especies también tuvieron grupos compuestos en su mayoría por prole que postergó su dispersión. En 3 especies hubo una presencia modesta, pero regular, de varias hembras (las hembras depositaron sus huevos en el mismo nido). Las 3 especies restantes se caracterizaron por tener aves de un año o subadultos. En más de la mitad de las especies, los grupos no parecían estar compuestos por individuos emparentados, contrario a lo que se observa en muchas aves paserinas que crían cooperativamente donde los grupos se conforman principalmente de prole que ha postergado su dispersión. Nuestra revisión sugiere que en muchas rapaces la evolución de la convivencia grupal puede ser independiente de la dispersión postergada, y que los factores más importantes que explican la evolución de este comportamiento dependen de los beneficios que ofrece la vida en grupo.

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COOPERATIVE BREEDING, in which more than two individuals participate in raising the offspring from a single nest, is found in ~3% of avian species (Brown 1987, Arnold and Owens 1998). Group composition and whether matings are monogamous or polygamous varies among and within species (reviewed in Brown 1987, Stacey and Koenig 1990, Emlen 1991, Cockburn 1996, Ligon 1999). The majority of well-studied cooperative breeding species live in groups composed of a behaviorally dominant breeding pair as well as additional helpers of either sex. The helpers are frequently offspring of the breeding pair who have delayed dispersal and so may be full or half-siblings of the offspring that they help to rear. Recent molecular evidence confirms that behavioral dominants largely monopolize reproduction, with reproduction by subordinates occurring only under certain circumstances (e.g. Rabenold et al. 1990, Dunn et al. 1995, Haydock et al. 1996, Lundy et al. 1998). Less common is cooperative polyandry, in which multiple adult males and a single adult female form a group. Generally, all males participate in copulations with the female, thus any males in a group may sire offspring and are potentially related to the offspring they assist in rearing. Finally, there are polygynandrous (or communal) groups, composed of multiple females and males, in which all group members may contribute genetically to the offspring produced by the group.

For many species that breed cooperatively, the specific mating system is not static or easily characterized. For example, group members may include both retained offspring (typical cooperative breeding) and multiple same-sex, unrelated adults that may all participate in copulations (e.g. Jamieson et al. 1994, Bednarz 1995, Malan et al. 1997, Whittingham et al. 1997, Lundy et al. 1998). Thus, we use the term "cooperative breeding" for all situations where individuals breed in groups.

Cooperative breeding has been of interest to evolutionary biologists because group breeding generally requires some individuals to forgo or share reproductive opportunities, potentially leading to a reduction in lifetime reproductive success. In many studies, that question why breed in groups? is treated as equivalent to why offspring should delay dispersal, and several authors (e.g. Cockburn 1996, Hatchwell and Komdeur 2000) have suggested

that the first step in the evolution of cooperative breeding is the evolution of delayed dispersal. Therefore, research in that area has been focused on understanding constraints limiting dispersal and the benefits of philopatry (Emlen 1982; Stacey and Ligon 1987, 1991; Koenig et al. 1992; Ligon 1999; Hatchwell and Komdeur 2000; Pen and Weissing 2000; Ekman et al. 2001; Russell 2001). After breeding occurs in groups that have evolved, there are many reasons why members of the group should aid in rearing both related and unrelated offspring, including kin selection, access to mates, skill acquisition, formation of alliances, and membership in a group that may provide a variety of benefits (reviewed in Cockburn 1998).

In an attempt to better understand the factors that may lead to cooperative breeding, a large number of ecological and life-history factors (such as climate, geography, diet, dispersal, habitat availability, survivorship, and clutch size) have been investigated (e.g. Ford et al. 1988; Poiani and Jermin 1994; DuPlessis et al. 1995; Arnold and Owens 1998, 1999). However, although certain traits—such as survivorship, clutch size, and climate—appear to correlate with cooperative breeding in many taxa, there do not seem to be universal conditions that can explain the evolution of cooperative breeding across taxa and geographic regions (Ford et al. 1988; Poiani and Jermin 1994; DuPlessis et al. 1995; Arnold and Owens 1998, 1999).

There is a phylogenetic component to cooperative breeding, such that the majority of cooperative breeders are restricted to a few avian lineages (Russell 1989, Edwards and Naeem 1993, Arnold and Owens 1998). The importance of evolutionary history in the taxonomic distribution of cooperative breeding in extant species is further reinforced by observations that closely related species living in very different habitats may breed cooperatively, indicating that ecological conditions may not explain all incidences of cooperative breeding (e.g. Zack 1995, Ligon 2001). Although evolutionary history is important, most avian lineages that contain cooperatively breeding species also contain noncooperatively breeding species (Brown 1987, Arnold and Owens 1998, Edwards and Naeem 1993). In addition, for many species that breed cooperatively, some individuals breed in monogamous pairs, and incidence of cooperative breeding may vary among populations of

the same species. Thus, particular avian lineages may often be predisposed to cooperative breeding or group living, but other factors may be important in determining whether cooperative breeding actually occurs.

Among Falconiformes (American Ornithologists' Union 1998), there are several well-studied examples of cooperative breeding. The Galápagos Hawk (*Buteo galapagoensis*) has a cooperatively polyandrous mating system, where the multimale groups are composed of unrelated adult males that share paternity (Faaborg et al. 1995). The Harris's Hawk (*Parabuteo unicinctus*) and the Pale Chanting Goshawk (*Melierax canorus*) are also classified as cooperatively polyandrous, though both of those species groups may contain unrelated adult males, females, and retained offspring (e.g. Bednarz 1995, Malan et al. 1997).

Hypotheses to explain cooperative breeding in those raptors have been varied, and the most likely reason suggested for each species differs. For example, in *Buteo galapagoensis*, it has been suggested that groups of males may be necessary to acquire and defend a territory (Faaborg et al. 1980, Faaborg 1986, Faaborg and Bednarz 1990). In contrast, cooperative hunting is a key advantage in *Parabuteo unicinctus*, and the enhanced foraging efficiency of cooperative hunting probably set the stage for the development of cooperative breeding (Bednarz 1988, Faaborg and Bednarz 1990). In *Melierax canorus*, polyandrous groups are more likely to lay a second clutch than are monogamous pairs, co-breeders assist in nest defense, and cooperative hunting may increase both foraging success as well as quality and size of captured prey, all of which could favor living in groups (Malan and Jenkins 1996; Malan and Crowe 1996, 1997; Malan et al. 1997; Malan 1998). Those divergent hypotheses suggest that different factors have been responsible for evolution of cooperative breeding in those respective taxa.

To examine those issues in more depth, we review the literature on cooperative breeding in diurnal raptors. In addition to the three well-studied species discussed above, we review the literature for other species in which cooperative breeding is an occasional to common feature of the breeding system. We then examine details of each cooperative breeding system (where known) and distribution of that behavior among diurnal raptors.

INCIDENCE AND DISTRIBUTION OF COOPERATIVE BREEDING AMONG DIURNAL RAPTORS

We have listed all taxa for which we found at least one example of more than two individuals residing in a group during a nesting attempt (Table 1). Because the same group is likely to inhabit the same territory for multiple years (Newton 1979), the number of cases indicates a number of different territories in which cooperative breeding was observed, regardless of the number of years of observation. For species in which multiple females were present, we have only included those cases in which it was clear that only one nest was present. The one exception is *Haliaeetus albicilla* (Green et al. 1996), where it was not reported what proportion of multifemale territories contained one nest (and represented cooperative breeding) or two nests (representing typical polygyny). Thus, for that species, all multifemale territories were included. Helping behavior, which we define as any behavior that could improve the probability of rearing offspring successfully (including nest building, nest defense, provisioning of the female; as well as direct helping such as incubating, brooding, or feeding of offspring) was not observed or confirmed in all cases.

Data presented in Table 1 are probably an underestimate both in terms of the number of species included and in the frequency of cooperative breeding in a given species. Cooperative groups may be overlooked in raptors (e.g. Newton 1979, Packham 1985, Santana et al. 1986, Bednarz 1987) for several reasons: (1) there are few raptor studies involving banded birds; (2) many species have large territories, making it difficult for observers to see all individuals residing in the territory; (3) many raptors are sensitive to disturbance and will avoid their nest or behave abnormally when a human observer is present; and (4) distance between territories may make it difficult to monitor a large number of nests in enough detail necessary to detect cooperative behavior. In addition, because most raptors are thought to be monogamous, additional birds may be viewed by casual observers as transients and thus not recorded. Finally, many diurnal raptors have been poorly studied, and for some, there are no data on nesting or breeding behavior, especially for raptors in the tropics. For some of those poorly studied species, possible cooperative breeding

TABLE 1. Instances of trios or larger groups in Falconides; within each family, taxa are organized alphabetically.

| Species | No. groups (%) ^a | Sex ^b | Age ^c | Copulations ^d | Help ^e | Citations |
|---------------------------------|-----------------------------|------------------|------------------|--------------------------|-------------------|---|
| Accipitridae | | | | | | |
| <i>Accipiter cooperii</i> | 1 | M | SA | ? | Y | Boal and Spaulding 2000 |
| <i>Accipiter nisus</i> | 6 | F | A | E | ? | Jourdain 1924, 1928 |
| | 1 | F | A | E | ? | Greeves 1926 |
| | 7 (0.6%) | F | A | E | ? | Etheridge (<i>in</i> Newton 1986) |
| | 1 (1%) | F | A | E | ? | Robson (<i>in</i> Newton 1986) |
| | 4 (1.7%) | ? | ? | E | ? | Green (<i>in</i> Newton 1986) |
| <i>Aquila chrysaetos</i> | 1 | ? | ? | ? | ? | Laistal 1966 (<i>in</i> Bergo 1988) |
| | 1 (20%) | M? | A | Y? | Y | Bergo 1987; 1988 |
| <i>Aquila pomarina</i> | 1 | ? | A | ? | ? | Cramp and Simmons 1980 |
| <i>Buteo augur</i> | 1 | M | ? | Y | ? | Lendrum 1979 |
| | 2 (7%) | ? | ? | ? | ? | Clouet et al. 2000 |
| <i>Buteo galapagoensis</i> | Many (0–100%) | M | A | Y | Y | Faaborg 1986; Faaborg et al. 1980, 1995 |
| <i>Buteo jamaicensis</i> | 1 (2%) | F | ? | ? | Y | Wiley 1975 |
| | 1 | F | A | ? | Y | Santana et al. 1986 |
| <i>Buteo lineatus</i> | 1 | ? | ? | ? | ? | Ogden 1974 |
| <i>Buteo poecilochrous</i> | ? | M | ? | ? | ? | del Hoya et al. 1992; deVries pers. comm. |
| <i>Buteo regalis</i> | "sometimes" | ? | A | ? | ? | Houston (<i>in</i> Bechard and Schmutz 1995) |
| <i>Buteo swainsoni</i> | 1 | ? | A | ? | Y | Cash 1989 |
| | "small proportion" | M | SA,? | Y | Y | Woodbridge et al. 1995; Woodbridge (<i>in</i> England et al. 1997) |
| | "small proportion" | M | SA,? | Y | Y | Woodbridge (<i>in</i> England et al. 1997) |
| <i>Circus buffoni</i> | 6 | M | A | Y | Y | Bó (<i>in</i> Simmons 2000) |
| <i>Circus cyaneus</i> | 1 | F | A | E | Y | Picozzi 1983 |
| <i>Circus maurus</i> | 1 | F | A | ? | ? | Arnott (<i>in</i> Simmons 2000) |
| <i>Circus pygargus</i> | 1 | M | SA | ? | Y | Cormier 1990 |
| | 1 | M | A | ? | Y | Arroyo 1996 |
| <i>Gypaetus barbatus</i> | 1 (8%) | M | ? | Y? | Y | Elosegi 1988 |
| | 1 (10%) | M | A | Y | Y | Fasce et al. 1989 |
| | 5 (12%) | M | A | Y | Y | Heredia and Donazar 1990 |
| | 14 (19%) | ? | ? | ? | ? | del Hoya et al. 1992 |
| | 14 (15.2%) | M | A | Y | Y | Bertran and Margalida 2002 |
| <i>Haliaeetus albicilla</i> | 3 (4%) | F? | ? | ? | ? | Green et al. 1996 |
| <i>Haliaeetus leucocephalus</i> | 3? (3–5%) | ? | A | ? | ? | Sherrord et al. 1976 |
| | 1 | ? | A | ? | ? | Fraser et al. 1983 |
| | 1 | M | ? | ? | Y | Nye 1994 |
| | 1 | F? | A | ? | Y | Garcelon et al. 1995 |

TABLE 1. Continued.

| Species | No. groups (%) | ^a Sex ^b | Age ^c | Copulations ^d | Help ^e | Citations |
|---------------------------------|------------------|-------------------------------|------------------|--------------------------|-------------------|--|
| <i>Haliaeetus vociferoides</i> | 19 (42%) | M, F | A, I | Y | Y | Watson et al. 1999 |
| <i>Hamirostra melanosternon</i> | 4 (36%) | M | A | Y | ? | Tingay et al. 2002 |
| <i>Ictinia mississippiensis</i> | 1 | M | A | Y | ? | Cupper and Cupper 1981 |
| | 18 (8.6%) | ? | I | ? | Y | Parker and Ports 1982; Parker 1988 |
| | "occasionally" | ? | I | ? | Y | Glinski and Ohmart 1983 |
| | 14 (88%) | ? | I | ? | ? | Evans 1981 (<i>in</i> Parker 1999) |
| | "most" of 12 | ? | I | ? | ? | Shaw 1985 (<i>in</i> Parker 1999) |
| <i>Melierax canorus</i> | 20% | M | A, I | Y | Y | Malan et al. 1997 |
| <i>Milvulus milvus</i> | "occasionally" | ? | ? | ? | ? | Davies and Davis 1973 |
| <i>Neophron percnopterus</i> | 1 | M | ? | ? | ? | Perennou et al. 1987 |
| | 2 (5%) | M | A | Y | Y | Tella 1993 |
| | 2 (5%) | M | ? | ? | ? | Donázar and Ceballos (<i>in</i> Tella 1993) |
| <i>Pandion haliaetus</i> | 1 (6%) | F | A | ? | ? | Dennis 1983 |
| <i>Parabuteo unicinctus</i> | Many (0 – 50%) | M, F | A, I | Y | Y | Bednarz 1995 |
| <i>Pernis ptilorhus</i> | 1 | ? | ? | ? | ? | Steiner 1997 |
| <i>Rostrihamus sociabilis</i> | "rare occasions" | ? | ? | ? | Y | Sykes et al. 1995 |
| <i>Spizaetus bartelsi</i> | 1 (33%) | M | SA | ? | Y | Hadi pers. comm. |
| <i>Terathopus caudatus</i> | 1 | ? | SA | ? | ? | Moreau 1945 |
| | 1 | M? | ? | ? | ? | Brown 1953 |
| Falconidae | | | | | | |
| <i>Falco biarmicus</i> | "rarely" | M | A | ? | ? | del Hoya et al. 1992 |
| <i>Falco columbarius</i> | 15 (14%) | M? | I, ? | Y | Y | James and Oliphant 1986; Sodhi 1991; Warkentin et al. 1994 |
| <i>Falco mexicanus</i> | 3 "rare" | ? | A | ? | ? | Sitter 1983 (<i>in</i> Steenhof 1998) |
| <i>Falco naumanni</i> | "occasionally" | M | I | ? | Y | Cramp and Simmons 1980 |
| | 1 (4%) | F | A | G | ? | Tella et al. 1996 |
| <i>Falco peregrinus</i> | 1 | F | ? | ? | Y | Spofford 1969 |
| | 26 | F | I | ? | Y | Monneret 1983; 1988 |
| | "rare" | ? | ? | ? | ? | Ratcliffe 1993 |
| <i>Falco sparverius</i> | 1 | M | ? | ? | Y | Wegner 1976 |
| | 1 | ? | ? | ? | Y | Wilmers 1983 |
| <i>Falco subbuteo</i> | 3 | M | ? | ? | Y | Cramp and Simmons 1980 |
| <i>Falco tinnunculus</i> | 1 | M | ? | ? | ? | Cramp and Simmons 1980 |
| | 4 | M | A | Y | ? | Packham 1985 |
| <i>Ibycter americanus</i> | "often" | ? | ? | ? | ? | Skutch 1959 |
| | | ? | ? | ? | ? | Thiollay 1991 |

TABLE 1. Continued.

| Species | No. groups (%) | ^a Sex ^b | Age ^c | Copulations ^d | Help ^e | Citations |
|----------------------------------|----------------|-------------------------------|------------------|--------------------------|-------------------|--------------------------------|
| <i>Microhierax fringillarius</i> | 1 | ? | ? | ? | ? | del Hoya et al. 1992 |
| <i>Phalacrocorax australis</i> | 4 | M? | A | ? | Y | J. Meiburg pers. comm. |
| <i>Poliolierax semitorquatus</i> | ? | M | ? | ? | ? | Thomsett 1991 (in Arroyo 1996) |

^aNumber of nests with groups (percentage of the population that contained groups).

^bSex of extra individuals (F = Female, M = Male, ? = Unknown).

^cAge of extra individuals (A = Adult, SA = Subadult, I = Immature, ? = Unknown).

^dCopulations observed with extra individuals (Y = Yes, ? = Unknown, E = Number of eggs in nest suggested both females laid and thus may have copulated with the male, G = Genetic confirmation that two females laid in a single nest).

^eHelping observed by extra individuals (Y = Yes, ? = Unknown).

has already been suggested (e.g. *Buteo albonotus*; Wilson et al. 1993), but not yet confirmed. Those factors combined suggest that more instances of cooperative breeding are likely to be detected among diurnal raptors in the future.

At this point, it is possible to draw some conclusions with the available data. First, cooperative breeding is widespread within the diurnal raptors, occurring in 22 of 76 genera (29%) and 42 of 304 species (14%). Cooperative breeders are found in both the Accipitridae (26% of genera, 13% of species) and the Falconidae (50% of genera, 19% of species) and are absent only in the monospecific family Sagittariidae. Second, cooperative breeding among diurnal raptors is very diverse. Although group composition has not been well documented in many species, it is clear that groups in some species contain reproductive pairs with immature helpers, others contain groups with either immature or adult helpers, whereas still other species have groups composed entirely of adults, though the sex of the extra adults is usually male in some taxa and female in others (Table 1).

Compared to published estimates, the incidence of cooperative breeding among diurnal raptors is high. Arnold and Owens (1998) reviewed all known cooperatively breeding birds, including those species where cooperative breeding had only been observed once or a small number of times (cf. Table 1) and concluded that 3.2% of species exhibit the behavior. Using a binomial test, the observed levels of cooperative breeding within the diurnal raptors (13% of species) is significantly greater than the 3.2% that would be expected by chance ($P < 0.0001$). In addition, of 62 avian families with cooperative breeders, only 22 contained a greater proportion of cooperatively breeding species than did the Accipitridae and the Falconidae (Arnold and Owens 1998).

For most species in Table 1, the number of observations is quite low. For some of those species, such as the well-studied Red-tailed Hawk, the low incidence of cooperative breeding (Table 1) is likely to be representative of the species. However, in less well-studied species the incidence of cooperative breeding could be much higher than indicated by our review. Because observations on many species are limited, we will focus on 10 species (Table 2) where sufficient data exist to provide some understanding of the dynamics of the breeding

TABLE 2. Species which regularly breed cooperatively; data from Cramp and Simmons (1980); del Hoya et al. (1992); and references from Table 1.

| Species | Food taken | Foraging mode | Social foraging ^a | Migratory ^a | Distribution ^b |
|--|--------------------|---------------|------------------------------|------------------------|--------------------------------|
| Extra birds primarily adult males | | | | | |
| <i>Buteo poecilochrous</i> | insects, sm. verts | ground | ? | ? | <u>Tropical, high altitude</u> |
| <i>Buteo galapagoensis</i> | generalists | ground | ? | N | <u>Tropical, island</u> |
| <i>Gypaetus barbatus</i> | bones | ground | ? | N | <u>Temperate/Tropical</u> |
| <i>Haliaeetus vociferoides</i> | fish, sm. verts | ground/water | pairs | N | <u>Tropical, island</u> |
| <i>Melierax canorus</i> | rodents | ground | Y | N | <u>Temperate/Tropical</u> |
| <i>Nephron percnopterus</i> | generalist | ground | ? | N, Y | <u>Temperate/Tropical</u> |
| <i>Parabuteo unicinctus</i> | med. verts. | ground | Y | N | <u>Temperate/Tropical</u> |
| Extra birds immatures | | | | | |
| <i>Falco columbarius</i> | sm. birds, bats | aerial | pairs | Y | <u>Temperate</u> |
| <i>Falco peregrinus</i> | birds, mammals | aerial | pairs | N, Y | <u>Temperate/Tropical</u> |
| <i>Ictinia mississippiensis</i> | insects | aerial | Y | Y | <u>Temperate</u> |

^a Y = yes; N = no; ? = unknown.

^b The climate underlined indicates where cooperative breeding occurs.

system. Those include species in which there are multiple observations and at least 5% of one population exhibits cooperative breeding, or those situations where a relatively large number of observations exist but the frequency of cooperative breeding could not be ascertained. We have excluded taxa that may frequently breed cooperatively, but for which we have very limited data on group composition and dynamics (e.g. *Ibycter americanus*; Skutch 1959).

Species where cooperative breeding occurs regularly are found in both Accipitridae and Falconidae and exhibit diversity in group composition (Table 2). The majority of those species consist of groups in which the extra birds are primarily adult males. In some cases, the sex of all group members could not be determined, though extra birds were male whenever group composition could be determined. Three species (*Haliaeetus vociferoides*, *Melierax canorus*, and *Parabuteo unicinctus*) appear to exhibit both cooperative polyandry and typical cooperative breeding, having groups that contain male co-breeders (on the basis of observations of copulations among presumably unrelated adults, DNA analyses, or both), immature individuals that have delayed dispersal (on the basis of banding data), or both (Bednarz 1995, Malan et al. 1997, Watson et al. 1999, Tingay et al. 2002). In *Buteo galapagoensis*, groups are polyandrous, with all adult males in the group copulating with the female. In that species, different males may sire offspring within and between years (Faaborg et al. 1995). Cooperative polyandry is also likely in *Gypaetus barbatus*, where copula-

tions between the female and both males in a group were observed in all trios (Fasce et al. 1989, Heredia and Donázar 1990, Bertran and Margalida 2002). Observations in the remaining two species, *Neophron percnopterus* and *B. poecilochrous*, indicate cooperative polyandry (Tella 1993; Tj. deVries pers. comm).

Three species show a different pattern: additional group members are immature helpers, though the sex of the helper differs among taxa. In *Falco columbarius*, when the gender of extra birds could be determined, they were male; whereas in *F. peregrinus*, extra birds were female. In *Ictinia mississippiensis*, the sex of helpers is unknown. The genetic relationship between immature helpers and adults in the group are unknown for those species. In *F. columbarius*, copulations between the immature helper and the adult female have been observed regularly (James and Oliphant 1986, Sodhi 1991), though those copulations rarely, if ever, result in offspring (Warkentin et al. 1994). Assuming copulations are avoided among close relatives (e.g. Emlen 1995), those immature helpers are probably unrelated to the adults in their group. Species with immature-only helpers are primarily migratory or wander extensively after attaining independence (*F. peregrinus*; Cramp and Simmons 1980) whereas other cooperative breeding species are largely nonmigratory. Because immature individuals and adults migrate independently (Mueller et al. 2000), migratory species may be less likely to maintain family units, and that may explain some of the differences in the composition of groups among

raptor species. However, both male and female *F. peregrinus* are philopatric (Ambrose and Riddle 1988, Newton and Mearns 1988), and it is possible that yearling females return to help in their natal territory in that species.

The observation that helpers are immature individuals in those three species suggests that the helping relationship does not exceed two years (adult plumage is attained during the second prebasic molt in those species), because longer associations would be expected to result in groups containing a breeding pair and either immature or adult helpers. In contrast, observations among species with adult helpers or cobreeders indicate that groups may be stable over longer periods (e.g. Faaborg 1986, Faaborg and Bednarz 1990, Bednarz 1995, Faaborg et al. 1995), even in those species that primarily breed in monogamous pairs (e.g. Nye 1994, Garcelon et al. 1995). The hypothesized shorter term relationship in species with immature-only helpers suggests that the dynamics in those species may be different than cooperatively breeding diurnal raptors with adult-plumaged extra birds.

One other pattern that occurs regularly in a very small proportion of nests is laying by multiple females into one nest (Table 1). All of those species—*Accipiter nisus*, *Circus cyaneus* and *Falco naumanni*—are regularly polygynous (Newton 1986, Korpimäki 1988, Simmons 2000), with females typically laying in separate, widely distributed nests. Although those species are territorial and female–female aggression is thought to be important in separating the nests of polygynous females (e.g. Newton 1986), it is clear that females will tolerate joint-nesting in some cases.

EVOLUTION AND MAINTENANCE OF COOPERATIVE BREEDING IN DIURNAL RAPTORS

There have been many hypotheses to explain the evolution of cooperative breeding. In particular, researchers have focused on ecological constraints that inhibit dispersal or lead to greater benefits for individuals that delay dispersal. Diurnal raptors appear to be relatively unique in that, although the data reviewed here indicate a relatively high frequency of cooperative breeding, there is only one species yet identified in which groups commonly form through delayed dispersal of offspring (*Parabuteo unicinctus*; Dawson and Mannan 1991, Bednarz 1995). Even in species in which some offspring delay

dispersal, unrelated same-sex adults are also found in groups. Therefore, factors that have led to the evolution and maintenance of cooperative breeding in many or all diurnal raptor species are likely independent of delayed dispersal.

For both the evolution and maintenance of cooperative breeding in diurnal raptors, individual group members, on average, should benefit by breeding and living in groups, even for those group members that must forgo or share reproduction within the group. There are several factors that may favor cooperative breeding in raptors that are independent of delayed dispersal. Those include (1) patchy resources within or between years (Newton 1979, Parker and Ports 1982, Heredia and Donázar 1990, Faaborg and Bednarz 1990); (2) a limited number of suitable territories, so territory acquisition and defense is likely to favor groups (Faaborg 1986, Fasce et al. 1989, Faaborg and Bednarz 1990, Tella 1993, Garcelon et al. 1995, Malan and Jenkins 1996); (3) group hunting or foraging (Bednarz 1988, 1995; Malan 1998); (4) lack of mates leading to mate sharing or unmated helpers (Parker and Ports 1982); (5) low reproductive success in pairs (Bergo 1988); (6) increased survivorship in groups (Faaborg et al. 1980, Faaborg and Bednarz 1990); and (7) thermoregulation (del Hoya et al. 1992). Those benefits are not mutually exclusive, and it is likely that some species may gain multiple benefits in at least some years. In addition, the benefits may differ over time, and there may be certain times or conditions during which groups may not be beneficial (e.g. Faaborg and Bednarz 1990), though they may persist because of increased benefits obtained during other periods. Unfortunately, even in species where cooperative breeding has been well studied, few quantitative data have been collected that would allow discrimination among the proposed benefits.

Interestingly, some of the benefits that have been suggested as important to raptors have also been suggested as important in many typical cooperative breeding species (e.g. Emlen 1982, Koenig et al. 1992). If the conditions that have led to cooperative breeding among diurnal raptors are the same as those in many other avian lineages, and offspring that have delayed dispersal do occur in some raptor species (e.g. *Parabuteo unicinctus*, *Melierax canorus*, and *Haliaeetus vociferoides*), that raises the question as to why cooperative groups among diurnal

raptors are more likely to be composed of unrelated individuals than related offspring that have delayed dispersal.

Differences in group composition between diurnal raptors and other cooperative breeding species may be due to a combination of evolutionary history, ecology, and life history that may differ among species. If the benefits of group living occur prior to successful reproduction, which might occur if groups were necessary for the acquisition of breeding territories or for thermoregulation, coalitions of unrelated individuals may be favored by selection. For example, in *Buteo galapagoensis*, groups have been suggested to be necessary for territory acquisition (Faaborg and Bednarz 1990). Recent observations in that species indicate that new males occasionally join pre-existing groups (Donaghy Cannon 2001), which suggests that at least some benefits may be independent of group-territory acquisition. Alternatively, because adult helpers occur in a large number of species, there may be advantages to adult, rather than immature, group members. Because raptor prey may often be costly to obtain and deliver, experienced adults may provide a greater benefit to a group than immature helpers, and that could have favored groups formed from coalitions of unrelated individuals over those formed from delayed dispersal. After there has been selection for groups, other factors may determine group composition. Delayed dispersal may have evolved secondarily in species where increasing or maintaining group sizes is beneficial, survivorship of dispersing immature helpers is low, or there is relatively little parent-offspring conflict, (e.g. Kokko and Lundberg 2001, Kokko et al. 2001).

CONCLUSION

Cooperative breeding has been examined in detail in only a few diurnal raptors. Future studies of raptors, including studies that are not focused on behavior, should be careful to document trios and larger groups. When groups are observed, it will be critical to document the age and sex of group members as well as other relevant information. Studies that include marked individuals or use genetic methods to examine relatedness will be particularly important to our understanding of cooperative breeding in raptors. The development of models to explain

the evolution of group living and cooperative breeding independently of delayed dispersal are also likely to provide critical information, particularly when combined with studies designed to test alternative models. Collectively, those additional data and models should establish whether cooperative breeding among raptors truly differs from the behavior exhibited by other groups of cooperative breeders, as this initial survey suggests. That research may also establish whether benefits from group living, rather than delayed dispersal, explain the evolution of cooperative breeding among some nonraptor species as well.

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LITERATURE CITED

- AMBROSE, R. E., AND K. E. RIDDLE. 1988. Population dispersal, turnover, and migration of Alaska peregrines. Pages 677–684 in *Peregrine Falcon Populations: Their Management and Recovery* (T. J. Cade, J. H. Enderson, G. C. Thelander and C. M. White, Eds.). The Peregrine Fund, Boise, Idaho.
- AMERICAN ORNITHOLOGISTS' UNION. 1998. Check-list of North American Birds, 7th ed. American Ornithologists' Union, Washington, D.C.
- ARNOLD, K. E., AND I. P. F. OWENS. 1998. Cooperative breeding in birds: A comparative test of the life history hypothesis. *Proceedings of the Royal Society of London, Series B* 265:739–745.
- ARNOLD, K. E., AND I. P. F. OWENS. 1999. Cooperative breeding in birds: The role of ecology. *Behavioral Ecology* 10:465–471.
- ARROYO, B. 1996. A possible case of polyandry in Montagu's Harrier. *Journal of Raptor Research* 30:100–102.
- BECHARD, M. J., AND J. K. SCHMUTZ. 1995. Ferruginous Hawk (*Buteo regalis*). In *The Birds of North America*, no. 172 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- BEDNARZ, J. C. 1987. Pair and group reproductive success, polyandry, and cooperative breeding in Harris' Hawks. *Auk* 104:393–404.
- BEDNARZ, J. C. 1988. Cooperative hunting in Harris' Hawks (*Parabuteo unicinctus*). *Science* 239: 1525–1527.

- BEDNARZ, J. C. 1995. Harris' Hawk (*Parabuteo unicinctus*). In *The Birds of North America*, no. 146 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- BERGO, G. 1987. Territorial behaviour of Golden Eagle in western Norway. *British Birds* 80: 361–376.
- BERGO, G. 1988. Trios in the Golden Eagle *Aquila chrysaetos* (L.). *Fauna Norvegica, Series C Cinclus* 11:40–44.
- BERTAN, J., AND A. MARGALIDA. 2002. Social organization of a trio of Bearded Vultures (*Gypaetus barbatus*): Sexual and parental roles. *Journal of Raptor Research* 36:66–70.
- BOAL, C. W., AND R. L. SPAULDING. 2000. Helping at a Cooper's Hawk nest. *Wilson Bulletin* 112: 275–277.
- BROWN, J. L. 1987. *Helping and Communal Breeding in Birds: Ecology and Evolution*. Princeton University Press, Princeton, New Jersey.
- BROWN, L. H. 1953. On the biology of the large birds of prey of the Embu district, Kenya Colony. *Ibis* 95:74–114.
- CASH, K. J. 1989. Three adult Swainson's Hawks tending a nest. *Condor* 91:727–728.
- CLOUET, M., C. BARRAU, AND J.-L. GOAR. 2000. The diurnal Afro-alpine raptor community of the Ethiopian Balé Highlands. *Ostrich* 71:380–384.
- COCKBURN, A. 1996. Why do so many Australian birds cooperate: Social evolution in the Corvida. Pages 451–472 in *Frontiers of Population Ecology* (R. B. Floyd, A. W. Sheppard, and P. J. De Barro, Eds.). CSIRO Publishing, Melbourne, Australia.
- COCKBURN, A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics* 29: 141–177.
- CORMIER, J.-P. 1990. Un cas d'aide à l'élevage des jeunes de la part d'un mâle de deux ans chez le Busard cendré *Circus pygargus* (L.). *Alauda* 58:203–204.
- CRAMP, S., AND K. E. L. SIMMONS, Eds. 1980. *Handbook of the Birds of Europe, the Middle East, and North Africa*, vol. 2. Oxford University Press, Oxford.
- CUPPER, J., AND L. CUPPER. 1981. *Hawks in Focus: A Study of Australia's Birds of Prey*. Jaclin Enterprises, Mildura, Australia.
- DAVIES, P. W., AND P. E. DAVIS. 1973. The ecology and conservation of the Red Kite in Wales. *British Birds* 66:183–224; 241–270.
- DAWSON, J. W., AND R. W. MANNAN. 1991. Dominance hierarchies and helper contributions in Harris' Hawks. *Auk* 108:649–660.
- DEL HOYA, J., ELLIOTT A, J. SARGATAL, AND N. J. COLLAR, Eds. 1992. *Handbook of the Birds of the World*, vol. 2. Lynx Edicions, Barcelona, Spain.
- DENNIS, R. H. 1983. Population studies and conservation of Ospreys in Scotland. Pages 207–214 in *Biology and Management of Bald Eagles and Ospreys* (D. M. Bird, Ed.). Harpell Press, Quebec.
- DONAGHY CANNON, M. M. 2001. Breeding ecology of cooperatively polyandrous Galápagos Hawks (*Buteo galapagoensis*) on Santiago Island, Galápagos. M.S. thesis, Arkansas State University, Jonesboro.
- DUNN, P. O., A. COCKBURN, AND R. A. MULDER. 1995. Fairy-wren helpers often care for young to which they are unrelated. *Proceedings of the Royal Society of London, Series B* 259:339–343.
- DU PLESSIS, M. A., W. R. SIEGFRIED, AND A. J. ARMSTRONG. 1995. Ecological and life-history correlates of cooperative breeding in South African birds. *Oecologia* 102:180–188.
- EDWARDS, S. V., AND S. NAEEM. 1993. The phylogenetic component of cooperative breeding in perching birds. *American Naturalist* 141: 754–789.
- EKMANN, J., V. BAGLIONE, S. EGGERS, AND M. GRIESSER. 2001. Delayed dispersal: Living under the reign of nepotistic parents. *Auk* 118:1–10.
- ELOSEGI, I. 1988. Le gypaète barbu. Pages 51–68 in *Grands Rapaces et Corvidés des Montagnes d'Europe: Biologie, Écologie, Ethnographie, Conservation* (C. Dendaletche, Ed.). Centre Pyrénéen de Biologie et Anthropologie des Montagnes, Pau.
- EMLEN, S. T. 1982. The evolution of helping, I. An ecological constraints model. *American Naturalist* 119:29–39.
- EMLEN, S. T. 1991. Evolution of cooperative breeding in birds and mammals. Pages 301–337 in *Behavioural Ecology: An Evolutionary Approach*, 3rd ed. (J. R. Krebs and N. B. Davies, Eds.). Blackwell, Oxford.
- EMLEN, S. T. 1995. An evolutionary theory of the family. *Proceedings of the National Academy of Sciences, United States* 92:8092–8099.
- ENGLAND, A. S., M. J. BECHARD, AND C. S. HOUSTON. 1997. Swainson's Hawk (*Buteo swainsoni*). In *The Birds of North America*, no. 265 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- FAABORG, J. 1986. Reproductive success and survivorship of the Galápagos Hawk *Buteo galapagoensis*—Potential costs and benefits of cooperative polyandry. *Ibis* 128:337–347.
- FAABORG, J., AND J. C. BEDNARZ. 1990. Galápagos and Harris' Hawks: Divergent causes of sociality in two raptors. Pages 359–383 in *Cooperative*

- Breeding in Birds: Long Term Studies of Ecology and Behaviour (P. Stacey and W. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- FAABORG, J., T. DE VRIES, C. B. PATTERSON, AND C. R. GRIFFIN. 1980. Preliminary observations of the occurrence and evolution of polyandry in the Galápagos Hawk (*Buteo galapagoensis*). *Auk* 97: 581–590.
- FAABORG, J., P. G. PARKER, L. DELAY, T. DE VRIES, J. C. BEDNARZ, S. M. PAZ, J. NARANJO, AND T. A. WAITE. 1995. Confirmation of cooperative polyandry in the Galápagos Hawk (*Buteo galapagoensis*). *Behavioral Ecology and Sociobiology* 36:83–90.
- FASCE, P., L. FASCE, AND J. TORRE. 1989. Census and observations on the biology of the Bearded Vulture *Gypaetus barbatus* on the island of Corsica. Pages 335–339 in *Raptors in the Modern World* (B.-U. Meyburg and R. D. Chancellor, Eds.). World Working Group on Birds of Prey, Berlin.
- FORD, H. A., H. BELL, R. NIAS, AND R. NOSKE. 1988. The relationship between ecology and the incidence of cooperative breeding in Australian birds. *Behavioral Ecology and Sociobiology* 22: 239–249.
- FRASER, J. D., L. D. FRENZEL, J. E. MATHISEN, AND M. E. SHOUGH. 1983. Three adult Bald Eagles at an active nest. *Raptor Research* 17:29–30.
- GARCELON, D. K., G. L. SLATER, C. D. DANILSON, AND R. G. HELM. 1995. Cooperative nesting by a trio of Bald Eagles. *Journal of Raptor Research* 29: 210–213.
- GLINSKI, R. L., AND R. D. OHMART. 1983. Breeding ecology of the Mississippi Kite in Arizona. *Condor* 85:200–207.
- GREEN, R. E., M. W. PIENKOWSKI, AND J. A. LOVE. 1996. Long-term viability of the re-introduced population of the White-tailed Eagle *Haliaeetus albicilla* in Scotland. *Journal of Applied Ecology* 33:357–368.
- GREEVES, N. 1926. Nine eggs of Sparrow-hawk in same nest. *British Birds* 20:77.
- HATCHWELL, B. J., AND J. KOMDEUR. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour* 59: 1079–1086.
- HAYDOCK, J., P. G. PARKER, AND K. N. RABENOLD. 1996. Extra-pair paternity uncommon in cooperatively breeding Bicolored Wren, *Campylorhynchus griseus*. *Behavioral Ecology and Sociobiology* 38:1–16.
- HEREDIA, R., AND J. A. DONÁZAR. 1990. High frequency of polyandrous trios in an endangered population of Lammergeiers *Gypaetus barbatus* in northern Spain. *Biological Conservation* 53: 163–171.
- JAMES, P. C., AND L. W. OLIPHANT. 1986. Extra birds and helpers at the nest of Richardson's Merlins. *Condor* 88:533–534.
- JAMIESON, I. G., J. S. QUINN, P. A. ROSE, AND B. N. WHITE. 1994. Shared paternity among non-relatives is a result of an egalitarian mating system in a communally breeding bird, the Pukeko. *Proceedings of the Royal Society of London, Series B* 257:271–277.
- JOURDAIN, F. C. R. 1924. Two hen Sparrow-hawks laying together. *British Birds* 17:288–289.
- JOURDAIN, F. C. R. 1928. Bigamy in the Sparrow-hawk. *British Birds* 21:200–202.
- KOENIG, W. D., F. A. PITELKA, W. J. CARMEN, R. L. MUMME, AND M. T. STANBACK. 1992. The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* 67:111–150.
- KOKKO, H., R. A. JOHNSTONE, AND T. H. CLUTTON-BROCK. 2001. The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London, Series B* 268:187–196.
- KOKKO, H., AND P. LUNDBERG. 2001. Dispersal, migration, and offspring retention in saturated habitats. *American Naturalist* 157:188–202.
- KORPIMAKI, E. 1988. Factors promoting polygyny in European birds of prey—A hypothesis. *Oecologia* 77:278–285.
- LENDRUM, A. L. 1979. The Augur Buzzard in the matopos, Rhodesia. *Ostrich* 50:203–314.
- LIGON, J. D. 1999. *The Evolution of Avian Breeding Systems*. Oxford University Press, Oxford.
- LIGON, J. D. 2001. Family Phoeniculidae (Woodhoopoes). Pages 412–435 in *Handbook of the Birds of the World* (J. del Hoyo, A. Elliott and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.
- LUNDY, K. J., P. G. PARKER, AND A. ZAHAVI. 1998. Reproduction by subordinates in cooperatively breeding Arabian Bblers is uncommon but predictable. *Behavioral Ecology and Sociobiology* 43:173–180.
- MALAN, G. 1998. Solitary and social hunting in Pale Chanting Goshawk (*Melierax canorus*) families: Why use both strategies? *Journal of Raptor Research* 32:195–201.
- MALAN, G., AND T. M. CROWE. 1996. The diet and conservation of monogamous and polyandrous Pale Chanting Goshawks in the Little Karoo, South Africa. *South African Journal of Wildlife Research* 26:1–10.
- MALAN, G., AND T. M. CROWE. 1997. Perch availability and ground cover: Factors that may constitute suitable hunting conditions for Pale Chanting Goshawk families. *South African Journal of Zoology* 32:14–20.
- MALAN, G., T. M. CROWE, R. BIGGS, AND J. J. HERHOLDT. 1997. The social system of the Pale Chanting

- Goshawk *Melierax canorus*; Monogamy vs. polyandry and delayed dispersal. *Ibis* 139:313–321.
- MALAN, G., AND A. R. JENKINS. 1996. Territory and nest defense in polyandrous Pale Chanting Goshawks: Do co-breeders help? *South African Journal of Zoology* 31:170–176.
- MONNERET, R.-J. 1983. L'aide à l'élevage chez le faucon pèlerin. *Alauda* 51:241–250.
- MONNERET, R.-J. 1988. Changes in the Peregrine Falcon populations of France. Pages 201–213 in *Peregrine Falcon Populations: Their Management and Recovery* (T. J. Cade, J. H. Enderson, C. G. Thelander and C. M. White, Eds.). The Peregrine Fund, Boise, Idaho.
- MOREAU, R. E. 1945. On the Bataleur, especially at the nest. *Ibis* 87:224–249.
- MUELLER, H. C., N. S. MUELLER, D. D. BERGER, G. ALLEZ, W. ROBICHAUD, AND J. L. KASPAR. 2000. Age and sex differences in the timing of fall migration of hawks and falcons. *Wilson Bulletin* 112:214–224.
- NEWTON, I. 1979. *Population Ecology of Raptors*. Buteo Books, Vermillion, South Dakota.
- NEWTON, I. 1986. *The Sparrowhawk*. T. and A. D. Poyser, Calton.
- NEWTON, I., AND R. MEARNES. 1988. Population ecology of peregrines in south Scotland. Pages 651–665 in *Peregrine Falcon Populations: Their Management and Recovery* (T. J. Cade, J. H. Enderson, G. C. Thelander, and C. M. White, Eds.). The Peregrine Fund, Boise, Idaho.
- NYE, P. E. 1994. Polygamy in Bald Eagles. *Journal of Raptor Research* 28:63.
- OGDEN, J. C. 1974. Aspects of Red-shouldered Hawk nesting in southern Florida. *Florida Field Naturalist* 2:25–27.
- PACKHAM, C. 1985. Bigamy in the Kestrel. *British Birds* 78:194.
- PARKER, J. W. 1988. Mississippi Kite. Pages 166–186 in *Handbook of North American Birds* (R. S. Palmer, Ed.). Yale University Press, New Haven, Connecticut.
- PARKER, J. W. 1999. Mississippi Kite (*Ictinia mississippiensis*). In *The Birds of North America*, no. 402 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- PARKER, J. W., AND M. PORTS. 1982. Helping at the nest by yearling Mississippi Kites. *Raptor Research* 16:14–17.
- PEN, L., AND F. J. WEISSING. 2000. Towards a unified theory of cooperative breeding: The role of ecology and life history re-examined. *Proceedings of the Royal Society of London, Series B* 267:2411–2418.
- PERENNOU, C., M. FILY, AND D. CANTOURNET. 1987. Note sur un cas de polyandrie chez le Vautour percnoptère *Neophron percnopterus*. *Alauda* 55: 73–75.
- PICOZZI, N. 1983. Two hens, but a single nest—An unusual case of polygyny by hen harriers in Orkney. *British Birds* 76:123–128.
- POIANI, A., AND L. S. JERMIN. 1994. A comparative analysis of some life-history traits between cooperatively and non-cooperatively breeding Australian passerines. *Evolutionary Ecology* 8: 471–488.
- RABENOLD, P. P., K. N. RABENOLD, W. H. PIPER, J. HAYDOCK, AND S. W. ZACK. 1990. Shared paternity revealed by genetic analysis in cooperatively breeding tropical wrens. *Nature* 348: 538–540.
- RATCLIFFE, D. 1993. *The Peregrine Falcon*, 2nd ed. T. and A. D. Poyser, London.
- RUSSELL, A. F. 2001. Dispersal costs set the scene for helping in an atypical avian cooperative breeder. *Proceedings of the Royal Society of London, Series B* 268:95–99.
- RUSSELL, E. M. 1989. Co-operative breeding—A Gondwanan perspective. *Emu* 89:61–62.
- SANTANA, E. C., R. L. KNIGHT, AND S. A. TEMPLE. 1986. Parental care at a Red-tailed Hawk nest tended by three adults. *Condor* 88:109–110.
- SHERROD, S. K., C. M. WHITE, AND F. S. L. WILLIAMSON. 1976. Biology of the Bald Eagle on Amchitka Island, Alaska. *Living Bird* 15:143–182.
- SIMMONS, R. E. 2000. *Harriers of the World: Their Behaviour and Ecology*. Oxford University Press, New York.
- SKUTCH, A. F. 1959. Red-throated Caracara—The scourge of the wasps. *Animal Kingdom* 62: 8–13.
- SODHI, N. S. 1991. Pair copulations, extra-pair copulations, and intraspecific nest intrusions in Merlin. *Condor* 93:433–437.
- SPOFFORD, W. R. 1969. Extra female at nesting site. Pages 418–419 in *Peregrine Falcon Populations: Their Biology and Decline* (J. J. Hickey, Ed.). University of Wisconsin Press, Madison.
- STACEY, P. B., AND W. D. KOENIG, EDs. 1990. *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behaviour*. Cambridge University Press, Cambridge, United Kingdom.
- STACEY, P. B., AND J. D. LIGON. 1987. Territory quality and dispersal options in the Acorn Woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. *American Naturalist* 130:654–676.
- STACEY, P. B., AND J. D. LIGON. 1991. The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: Variation in territory quality and group-size effects. *American Naturalist* 137:831–846.
- STEENHOF, K. 1998. Prairie Falcon (*Falco mexicanus*). In *The Birds of North America*, no. 346 (A. Poole and F. Gill, Eds.). Academy of

- Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- STEINER, H. 1997. Ein trio beim Wespenbussard (*Pernis apivorus*). *Egretta* 40:45-47.
- SYKES, P. W. J., J. A. J. RODGERS, AND R. E. BENNETTS. 1995. Snail Kite (*Rostrhamus sociabilis*). In *The Birds of North America*, no. 171 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- TELLA, J. L. 1993. Polyandrous trios in a population of Egyptian Vultures. *Journal of Raptor Research* 27:119-120.
- TELLA, J. L., J. J. NEGRO, M. VILLARROEL, U. KUHNLEIN, F. HIRALDO, J. A. DONÁZAR, AND D. M. BIRD. 1996. DNA fingerprinting reveals polygyny in the Lesser Kestrel (*Falco naumanni*). *Auk* 113: 262-265.
- THIOLLAY, J.-M. 1991. Foraging, home range use and social behavior of a group-living rain forest raptor, the Red-throated Caracara *Daptrius americanus*. *Ibis* 133:382-393.
- TINGAY, R. E., M. CULVER, E. M. HALLERMAN, J. D. FRASER, AND R. T. WATSON. 2002. Subordinate males sire offspring in Madagascar Fish-Eagle (*Haliaeetus vociferoides*) polyandrous breeding groups. *Journal of Raptor Research* 36:280-286.
- WARKENTIN, I. G., A. D. CURZON, R. E. CARTER, J. H. WETTON, P. C. JAMES, L. W. OLIPHANT, AND D. T. PARKIN. 1994. No evidence for extrapair fertilizations in the Merlin revealed by DNA fingerprinting. *Molecular Ecology* 3:229-234.
- WATSON, R. T., S. RAZAFINDRAMANANA, R. THORSTROM, AND S. RAFANOMEZANTSOA. 1999. Breeding biology, extra-pair birds, productivity, siblicide and conservation of the Madagascar Fish-Eagle. *Ostrich* 70:105-111.
- WEGNER, W. A. 1976. Extra-parental assistance by male American Kestrel. *Wilson Bulletin* 88: 670.
- WHITTINGHAM, L. A., P. O. DUNN, AND R. D. MAGRATH. 1997. Relatedness, polyandry and extra-group paternity in the cooperatively-breeding White-browed Scrubwren (*Sericornis frontalis*). *Behavioral Ecology and Sociobiology* 40:261-270.
- WILEY, J. W. 1975. Three adult Red-tailed Hawks tending a nest. *Condor* 77:480-482.
- WILMERS, T. J. 1983. Kestrel use of nest boxes on reclaimed surface mines in West Virginia and Pennsylvania. *Raptor Research* 17:30-31.
- WILSON, B. E., C. COLDREN, M. COLDREN, F. CHAVEZ-RAMIREZ, AND T. ARCHER. 1993. Behavior of a group of Zone-tailed Hawks. *Journal of Raptor Research* 27:127.
- WOODBIDGE, B., K. K. FINLEY, AND P. H. BLOOM. 1995. Reproductive performance, age structure, and natal dispersal of Swainson's Hawk in the Butte Valley, California. *Journal of Raptor Research* 29:187-192.
- ZACK, S. 1995. Cooperative breeding in *Lanius* shrikes, III. A reply in hindsight to Zack and Ligon I, II (1985). *Proceedings of the Western Foundation of Vertebrate Zoology* 6:34-38.

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