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PROLONGED INCUBATION IN RAPTORS: ADAPTIVE OR NONADAPTIVE BEHAVIOR?

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During the incubation period, energy demands may be relatively high on raptors and incubating parents in at least some species suffer energetic stress, thus increasing mortality (Siikamäki 1995). Because incubation behavior precludes foraging, energy constraints may be significant (Reid et al. 2002). In many species, incubation results in a loss of body mass (e.g., Newton 1979, Wendeln and Becker 1996, Kilpi and Lindstrom 1997), and this may be noticeable in females that experience longer-than-average incubation periods (Tombre and Erikstad 1996). In addition, incubating birds probably face an increased mortality risk to predators at the nest (e.g., Lima 1998, Wiebe and Martin 1998, Weidinger 2002, Amat and Masero 2004a). Therefore, the duration of incubation should be as short as possible, provided that the development and survival of offspring are not compromised.

Intraspecific variation in the duration of incubation has been reported in many avian species and is typically negatively related to variation in parental attentiveness, with longer periods for those clutches incubated less attentively (Lifjeld and Slagsvold 1986, Lifjeld et al. 1987). Abnormally long incubation periods leading to viable hatchlings have been documented in several species of birds (Skutch 1962, Holcomb 1970). Large within-species variation in the duration of incubation is particularly common in Procellariiformes (e.g., Boersma and Wheelwright 1979, Warham 1990, Chaurand and Weimerskirch 1994, Huin 1997). The generally accepted explanation for this phenomenon in this group has been related to intermittent incubation, or egg neglect, as a consequence of long foraging distances (Boersma and Wheelwright 1979). Embryos from neglected eggs develop more slowly (Astheimer 1991), thus taking longer to hatch. Within-species variation in incubation duration of hatchable eggs in other groups of birds has also been described in relation to clutch size (with longer periods needed for larger clutches), body size (longer periods for smaller birds), and hatching asynchrony (longer periods for clutches in which nestlings hatch asynchronously; e.g., Magrath 1992, Bortolotti and Wiebe 1993, Sandercock 1997, Eikenaar et al. 2003). Parental nest attendance and incubation duration can also be affected by ambient temperatures (Conway and Martin 2000, Amat and Masero 2004b) and by contaminants in parents, which may reduce incubating efficiency (Fisher et al. 2006). Time spent incubating can increase with greater food availability (Drent et al. 1985, Rauter and Reyer 1997) and when males provision incubating females on the nest (Nilsson and Smith 1988, Halupka 1994, Hatchwell et al. 1999).

Prolonged incubation (i.e., abnormally longer than mean incubation periods) of unhatchable eggs has also been described in several species of birds (e.g., Skutch 1962, Holcomb 1970, Kloskowski 1999, Nuechterlein and Buitron 2002), sometimes for very long periods (e.g., 175% longer than the mean of the normal incubation time for the European Shag [*Phalacrocorax aristotelis*]; Skutch 1962). Understanding why birds incubate nonviable eggs may help us better understand the regulation of incubation behavior. Prolonged incubation is thought to be an adaptive mechanism that provides a margin of safety for eggs that take longer than normal to hatch (Holcomb 1970, Huin 1997). However, excessively long incubation periods have been considered maladaptive for birds that

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could otherwise renest after a breeding failure (Skutch 1962, Holcomb 1970, Marks 1983). Prolonged incubation is potentially costly due to increased predation risk and loss of body mass, both detrimental for future adult survival or reproduction. The balance between costs and benefits of this behavior should vary with ecological and life history characteristics of species.

As a safety mechanism for ensuring hatchability of the current breeding attempt, but potentially costly in terms of future reproduction, we predict that prolonged incubation should be more common in species that cannot renest than in those that can. We also predict that this behavior should be more common in species with low predation risk (e.g., in larger than in smaller species, and in cavity versus open nesters). Marks (1983) suggested that prolonged incubation behavior is related to the time interval in which an entire clutch would normally hatch and that species with large clutches that hatch asynchronously may be more likely to prolong incubation than species whose eggs hatch in a short time interval. In this sense, we predict that species that hatch their eggs asynchronously may have more conflict about when to stop incubating unhatched eggs, because these species may have a naturally wider within-species variation in incubation duration for viable eggs. Finally, we predict that prolonged incubation should occur more often in species with assisted gyneparental incubation (male providing food to his mate but does not incubate) than in species with biparental continuous incubation (Williams 1996), given that in the former there is no need for the incubating bird to choose between attending the eggs and foraging.

Raptors are a good group to evaluate these predictions because there is a great deal of variation among species in terms of predation risk, a gradient not present in many other groups. In addition, raptors have variation in the levels of gender role partitioning, and are also variable in terms of renesting potential. Most species of raptors have multi-egg clutches, and so some intraspecific variation in the length of the incubation period should exist due to clutch size, egg-size, body size, and hatching asynchrony (Bortolotti and Wiebe 1993, Viñuela 1997, Wiebe et al. 1998). Here we provide a review of available information for diurnal and nocturnal raptors, and raise questions about this behavior that may stimulate researchers to gather more information to test some of the above-stated hypotheses.

We have used data from published studies, as well as personal observations or unpublished information provided by fellow raptor researchers, referring to prolonged incubation. We use only cases where monitoring was intensive and it was known with reasonable precision the length of incubation (i.e., both laying date and abandonment date) or the minimum length of incubation (i.e., laying date was not known, but the incubation length was longer than the normal). Only first clutches were considered.

As shown in Table 1, prolonged incubation of eggs that did not hatch has been observed in many species in a wide range of genera. Two factors may lead to nonviability of eggs: infertility and embryo death. It is well known that eggs have a narrow range of thermal tolerance for exposures lasting several hours (36–39°C; Webb 1987). The lack of attendance at the nest or inefficient incubating behavior may therefore cause embryo death. The thermal tolerance of eggs to temperature fluctuations varies among species and the different incubation patterns may reflect this sensitivity.

As previously stated, prolonged incubation could be an adaptive mechanism to ensure egg hatching, and indeed successful hatching of eggs after an incubation period 40% longer than mean has been observed in American Kestrels (*Falco sparverius*; J. Smits pers. comm.). However, it is probably detrimental to continue incubation of addled eggs, particularly in species that can renest after clutch failure, or in species that suffer predation or food stress while incubating. We evaluate the available information in relation to the predictions stated above.

Overall, prolonged incubation was reported both in relatively small species with potentially high predation risk (e.g., Lesser Kestrel [*Falco naumanni*], Eurasian Sparrowhawk [*Accipiter nisus*], and Montagu's Harrier [*Circus pygargus*]), and in large raptors in which incubating birds would not in principle be exposed to high predation risk (e.g., vultures and eagles). Prolonged incubation has also been documented both in species in which relaying is rare or nonexistent (e.g., Eurasian Griffon [*Gyps fulvus*], Bearded Vulture [*Gypaetus barbatus*]), and in species in which relaying can occur frequently (e.g., Montagu's Harrier, Lesser Kestrel), suggesting that this behavior is independent of the probability of future nesting at the species level. Another indication that prolonged incubation may be independent of the likelihood of future reproduction is that, at least in the Bearded Vulture, this behavior has been documented in territories with different breeding experience (Table 1; Margalida et al. 2003); older birds with fewer future reproductive opportunities would be expected to devote a greater effort to the current reproductive attempt than younger birds (Williams 1966). Additionally, prolonged incubation also occurred both in raptor species with biparental continuous incubation such as vultures (where incubation conflicts more directly with foraging), and in species with assisted gyneparental incubation such as falcons, harriers, eagles, and kites.

Prolonged incubation has been documented both in species with small, fixed clutch sizes or with a small degree of hatching asynchrony (e.g. Eurasian Griffon, Bearded Vulture, Bonelli's Eagle [*Hieraaetus fasciatus*], Spanish Imperial Eagle [*Aquila adalberti*]) and in species with large, variable clutch sizes in which the degree of hatching asynchrony varies greatly between clutches (e.g., Montagu's Harrier, Lesser Kestrel, American Kestrel).

Therefore, data in Table 1 did not support any of our predictions. One of the limitations of our analysis is that this behavior has not been documented well enough in the literature to calculate the frequency of occurrence within

Table 1. Details of prolonged incubation in species of diurnal and nocturnal raptors.

SPECIES	MEAN LENGTH OF INCUBATION PERIOD	MAXIMUM DAYS OF PROLONGED INCUBATION OBSERVED	DAYS LONGER THAN MEAN (%)	SOURCE
Accipitridae				
Golden Eagle (*Aquila chrysaetos*)	44	115	71 (161)	Brown 1976b
Spanish Imperial Eagle (*Aquila adalberti*)	44	>75	>31 (>70)	R. Sánchez pers. comm.
Verreaux's Eagle (*Aquila verreauxii*)	45	60	15 (33)	Gargett 1990
Bearded Vulture (*Gypaetus barbatus*)	54	127	73 (135)	A. Margalida unpubl. data
Eurasian Griffon Vulture (*Gyps fulvus*)	52	107	55 (106)	Leconte and Som 1996
Bonnelli's Eagle (*Hieraaetus fasciatus*)	40	70	30 (75)	J. Real unpubl. data
Bald Eagle (*Haliaaetus leucocephalus*)	35	60	25 (71)	Broley 1947
Eurasian Sparrowhawk (*Accipiter nisus*)	33	66	33 (100)	Newton 1986
Red-shouldered Hawk (*Buteo lineatus*)	33	56	23 (70)	Covert 1949 in Palmer 1988
Black Kite (*Milvus migrans*)	30	50	20 (67)	Viñuela 1991
Montagu's Harrier (*Circus pygargus*)	30	>48	>18 (>60)	B.E. Arroyo unpubl. data
Northern Harrier (*Circus cyaneus*)	32	70	38 (118)	Brown 1976a
Falconidae				
Peregrine Falcon (*Falco peregrinus*)	30	>73	>43 (>143)	Martin and North 1993
Lesser Kestrel (*Falco naumanni*)	27	>50	>23 (>85)	J. Aparicio and R. Bonal unpubl. data
Common Kestrel (*Falco tinnunculus*)	31	>48	>17 (>55)	J. Aparicio unpubl. data
American Kestrel (*Falco sparverius*)	28	>43	>15 (>54)	G. Bortolotti unpubl. data
Strigidae				
Long-eared Owl (*Asio otus*)	26–28	65	37 (137)	Marks 1983
Tytonidae				
Barn Owl (*Tyto alba*)	33	84	51 (155)	East 1930

a species. Most predictions refer to the frequency of occurrence because it is expected that attributes of individuals will influence the likelihood of continuing incubation; e.g., birds in poor condition may not be able to afford long incubation periods.

We suggest that observers should not, as some do, remove eggs after what appears to be a normal incubation period, but rather document and monitor such failed nests. Further investigation into prolonged incubation will shed light on the mechanisms regulating incubation behavior. Hormones are important proximate factors regulating incubation behavior. A rise in prolactin is associated with the onset and maintenance of incubation and care of young (Buntin 1996). Levels of prolactin are usually higher in incubating than in non-incubating birds (e.g., in Harris's Hawks [*Parabuteo unicinctus*] females have more than twice the levels of males; Vleck et al. 1991). The continuity of incubation of addled eggs may be associated with high levels of the hormones that stimulate this behavior (Collias and Collias 1984). Additionally, there is natural variation in the length of incubation, and extremely long incubations have resulted in viable hatchings (J. Smits pers. comm.). Therefore, it may pay to prolong incubation to a certain extent. In contrast, at least two other factors could lead to relatively short incubation periods, and lead parents to desert addled eggs: (1) embryonic vocalizations, usual during late incubation, and which allow parents to assess egg viability and thus preventing their abandonment (Brua et al. 1996); (2) the time and energy demands during the incubation period that can represent an important component of reproductive cost for parents (Reid et al. 2002).

Our review suggests that prolonged incubation in raptors occurs in many species. Quantitative data on the frequency of this behavior will enable statistical tests on how it is related to individual attributes or ecological variables, and will help us better understand the regulation of incubating behavior in birds.

INCUBACION PROLONGADA EN RAPACES: COMPORTAMIENTO ADAPTATIVO O NO ADAPTATIVO?

RESUMEN.—Presentamos una revisión de casos descritos de incubación prolongada en diferentes especies de rapaces, tanto diurnas como nocturnas. Siendo un mecanismo para asegurar que los huevos eclosionen, la incubación prolongada también presenta costos potenciales en términos de la reproducción futura relacionados con la posible pérdida de condición durante la incubación, los riesgos de depredación o las posibilidades de volver a criar en la misma temporada reproductiva. Por ello, la incubación prolongada debería observarse más frecuentemente en especies con bajo riesgo de depredación, sin reemplazo de puestas, con poca asincronía en la eclosión y con cuidado parental compartido. Evaluamos estas hipótesis con datos existentes para diferentes especies. La información compilada que presentamos sugiere que la incubación prolongada de huevos que no eclosionan parece ser un hecho habitual, y no se conoce si se trata de un comportamiento adaptativo. Sería necesario disponer de datos cuantitativos sobre la frecuencia de este comportamiento a nivel de especies para poder probar si éste es atribuible a las características individuales de las especies o está relacionado con variables ecológicas.

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LITERATURE CITED

AMAT, J.A. AND J.A. MASERO. 2004a. Predation risk on incubating adults constraints the choice of thermally favourable nest sites in a plover. *Anim. Behav.* 67:293–300.

——— AND ———. 2004b. How Kentish Plovers, *Charadrius alexandrinus,* cope with heat stress during incubation. *Behav. Ecol. Sociobiol.* 56:26–33.

ASTHEIMER, L.B. 1991. Embryo metabolism and egg neglect in Cassin's Auklets. *Condor* 93:486–495.

BOERSMA, P.D. AND N.T. WHEELWRIGHT. 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the Fork-tailed Storm-Petrel. *Condor* 81:157–165.

BORTOLOTTI, G.R. AND K.L. WIEBE. 1993. Incubation behaviour and hatching patterns in the American Kestrel *Falco sparverius. Ornis Scand.* 24:41–47.

BROLEY, C.L. 1947. Migration and nesting of Florida Bald Eagles. *Wilson Bull.* 59:1–68.

BROWN, L. 1976a. Birds of prey. Chancellor Press, London, United Kingdom.

———. 1976b. Eagles of the world. Universe Books, New York, U.S.A.

BRUA, R.B., G.L. NUECHTERLEIN, AND D. BUITRON. 1996. Vocal response of Eared Grebe embryos to egg cooling and egg turning. *Auk* 113:525–533.

BUNTIN, J.D. 1996. Neural and hormonal control of parental behavior in birds. *Adv. Study Behav.* 25:161–213.

CHAURAND, T. AND H. WEIMERSKIRCH. 1994. Incubation routine, body mass regulation and egg neglect in the Blue Petrel *Halobaena caerulea. Ibis* 136:285–290.

COLLIAS, N.E. AND E.C. COLLIAS. 1984. Nest building and bird behaviour. Princeton University Press, Princeton, NJ U.S.A.

CONWAY, C. AND T.E. MARTIN. 2000. Effects of ambient temperature on avian incubation behavior. *Behav. Ecol.* 11:178–188.

DRENT, R.H., J.M. TINBERGEN, AND H. BIEBACH. 1985. Incubation in the starling *Sturnus vulgaris*: resolution of the conflict between egg care and foraging. *Neth. J. Zool.* 35:103–123.

EAST, B. 1930. My friends of the sycamore. *Bird Lore* 32: 4–7.

EIKENAAR, C., M.L. BERG, AND J. KOMDEUR. 2003. Experimental evidence for the influence of food availability on incubation attendance and hatching asynchrony in the Australian Reed Warbler *Acrocephalus australis. J. Avian Biol.* 34:419–427.

FISHER, S.A., G.R. BORTOLOTTI, K.J. FERNIE, D.M. BIRD, AND J.E. SMITS. 2006. Behavioral variation and its consequences during incubation for American Kestrels exposed to PCBs. *Ecotoxicol. Environ. Saf.* 63:226–235.

GARGETT, V. 1990. The Black Eagle, a study. Academic Press, London, United Kingdom.

HALUPKA, K. 1994. Incubation feeding in Meadow Pipit *Anthus pratensis* affects female time budget. *J. Avian Biol.* 25:251–253.

HATCHWELL, B.J., M.K. FOWLIE, D.J. ROSS, AND A.F. RUSSELL. 1999. Incubation behaviour of Long-tailed Tits: why do males provision incubating females? *Condor* 101: 681–686.

HOLCOMB, L.C. 1970. Prolonged incubation behaviour of Red-winged Blackbird incubating several egg sizes. *Behaviour* 36:74–83.

HUIN, N. 1997. Prolonged incubation in the Black-browed Albatross *Diomedea melanophris* at South Georgia. *Ibis* 139:178–180.

KILPI, M. AND K. LINDSTROM. 1997. Habitat-specific clutch size and cost of incubation in Common Eiders, *Somateria mollissima*. *Oecologia* 111:297–301.

KLOSKOWSKI, J. 1999. Prolonged incubation of unhatchable eggs in Red-necked Grebes (*Podiceps grisegena*). *J. Ornithol.* 140:101–104.

LECONTE, M. AND J. SOM. 1996. La reproduction du vautour fauve (*Gyps fulvus*) dans les Pyrénées occidentales: historique d'une restauration d'effectifs et paramètres reproducteurs. *Alauda* 64:135–148.

LIFJELD, J.T. AND T. SLAGSVOLD. 1986. The function of courtship feeding during incubation in the Pied Flycatcher *Ficedula hypoleuca*. *Anim. Behav.* 34:1441–1453.

———, ———, AND G. STENMARK. 1987. Allocation of incubation feeding in a polygynous mating system: a study on Pied Flycatchers *Ficedula hypoleuca*. *Anim. Behav.* 35:1663–1669.

LIMA, S.L. 1998. Stress and decision making under risk of predation: recent developments from behavioural, reproductive, and ecological perspectives. *Adv. Study Behav.* 27:215–290.

MAGRATH, R.D. 1992. Roles of egg mass and incubation pattern in establishment of hatching hierarchies in the Blackbird (*Turdus merula*). *Auk* 109:474–487.

MARGALIDA, A., D. GARCÍA, J. BERTRAN, AND R. HEREDIA. 2003. Breeding biology and success of the Bearded Vulture *Gypaetus barbatus* in the eastern Pyrenees. *Ibis* 145: 244–252.

MARKS, J.S. 1983. Prolonged incubation by a Long-eared Owl. *J. Field Ornithol.* 54:199–200.

MARTIN, C.J. AND D.J. NORTH. 1993. Peregrine falcons incubate clutch of eggs for minimum of 73 days. *J. Raptor Res.* 27:173.

NEWTON, I. 1979. Population ecology of raptors. T. & A.D. Poyser, Berkhamsted, United Kingdom.

———. 1986. The sparrowhawk. T. & A.D. Poyser, Calton, United Kingdom.

NILSSON, J.A. AND H.G. SMITH. 1988. Incubation feeding as a male tactic for early hatching. *Anim. Behav.* 36:641–647.

NUECHTERLEIN, G.L. AND D. BUITRON. 2002. Nocturnal egg neglect and prolonged incubation in the Red-necked Grebe. *Waterbirds* 25:485–491.

PALMER, R.S. 1988. Handbook of North American birds. Vol. 4. Yale University Press, New Haven, CT U.S.A.

RAUTER, C. AND H.-U. REYER. 1997. Incubation pattern and foraging effort in female Water Pipit *Anthus spinoletta*. *Ibis* 139:441–446.

REID, J.M., P. MONAGHAN, AND R.G. NAGER. 2002. Incubation and the costs of reproduction. Pages 314–325 *in* D.C. Deeming [ED.], Avian incubation. Behaviour, environment, and evolution. Oxford University Press, Oxford, United Kingdom.

SANDERCOCK, B.K. 1997. Incubation capacity and clutch size determination in two calidrine sandpipers: a test of the four-egg threshold. *Oecologia* 110:50–59.

SIIKAMÄKI, P. 1995. Are large clutches costly to incubate? The case of the Pied Flycatcher. *J. Avian Biol.* 26:76–80.

SKUTCH, A.F. 1962. The constancy of incubation. *Wilson Bull.* 74:115–152.

TOMBRE, I.M. AND K.E. ERIKSTAD. 1996. An experimental study of incubation effort in high-Arctic Barnacle Geese. *J. Anim. Ecol.* 65:325–331.

VIÑUELA, J. 1991. Ecología reproductiva del Milano Negro (*Milvus migrans*) en el Parque Nacional de Doñana. M.S. thesis, Universidad Complutense de Madrid, Madrid, Spain.

———. 1997. Laying order affects incubation duration in the Black Kite (*Milvus migrans*): counteracting hatching asynchrony? *Auk* 114:192–199.

VLECK, C.M., N.A. MAYS, J.W. DAWSON, AND A.R. GOLDSMITH. 1991. Hormonal correlates of parental and helping behavior in cooperatively breeding Harris' Hawks (*Parabuteo unicinctus*). *Auk* 108:638–648.

WARHAM, J. 1990. The petrels, their ecology and breeding systems. Academic Press, London, United Kindom.

WEBB, D.R. 1987. Thermal tolerance of avian embryos: a review. *Condor* 89:874–898.

WEIDINGER, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *J. Anim. Ecol.* 71:424–437.

WENDELN, H. AND P.H. BECKER. 1996. Body mass change in breeding Common Terns *Sterna hirundo*. *Bird Study* 43:85–95.

WIEBE, K.L., J. WIEHN, AND E. KORPIMÄKI. 1998. The onset of incubation in birds: can females control hatching patterns? *Anim. Behav.* 55:1043–1052.

——— AND K. MARTIN. 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. *Anim. Behav.* 56:1137–1144.

WILLIAMS, G.C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, NJ U.S.A.

WILLIAMS, J.B. 1996. Energetics of avian incubation. Pages 375–416 *in* C. Carey [ED.], Avian energetics and nutritional ecology. Chapman and Hall, New York, U.S.A.

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