

The Insurance-egg Hypothesis and Extra Reproductive Value of Last-laid Eggs in Clutches of American Kestrels

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Many species of birds lay more eggs than they normally rear to independence. This is illustrated well by species with obligate siblicide, such as eagles (Meyburg 1974) and boobies (Anderson 1990), where the youngest nestling in a brood is killed by its older sibling in a physical struggle soon after hatching. A common explanation for such behavior is that parents can raise only one offspring, but lay the extra egg for insurance against infertility (the insurance-egg hypothesis; Dorward 1962); the surplus offspring is eliminated if its older sibling is viable. Field experiments testing the insurance-egg hypothesis have been performed for a few species with obligate siblicide (e.g. Cash and Evans 1986, Anderson 1990).

Until recently, the insurance value of offspring was not considered to be important for birds with facultative siblicide (i.e. where survival of youngest offspring is conditional on prevailing environmental conditions). Such offspring usually were thought to be an adaptation to an environment where food was unpredictable at the time of laying. Parents could rear the entire brood if food proved to be abundant, but if food was scarce, they could eliminate the extra offspring through brood reduction (Lack 1947, Ricklefs 1965; called "resource tracking" by Forbes 1991). Mock and Parker (1986) emphasized that the youngest nestling in a brood may serve two simultaneous functions in species with facultative brood reduction: resource tracking and insurance. The costs and benefits of insurance offspring have been modelled in a general way by Forbes (1990, 1991); extra offspring may provide multiple benefits simultaneously (Mock and Forbes 1995). Here, I examine the value of the last-laid egg in broods of American Kestrels (*Falco sparverius*), a species with facultative brood reduction.

Methods.—From 1988 to 1992, coworkers and I studied a population of about 200 pairs of American Kestrels breeding in nest boxes at Besnard Lake, Saskatchewan (55°20'N, 106°W). Details about the study site and nest boxes are summarized in Bortolotti et al. (1991) and Bortolotti (1994). Each year, adults in the population were trapped, banded, and measured (see Wiebe and Bortolotti 1993); by visiting boxes regularly, we recorded the reproductive performance of most parents. In many nests, eggs were numbered according to laying sequence with nontoxic felt markers, and nestlings were similarly marked according to hatching order (Wiebe and Bortolotti 1995a, b). The

growth and survival of nestlings were recorded during visits to the nest boxes at least once every three days (Wiebe and Bortolotti 1995a).

I partitioned the total reproductive value (RV_{tot}) of the last-laid egg of a clutch into two components. As described by Mock and Parker (1986), the extra egg has insurance value whenever the resulting chick survives to replace an older egg or chick that has died, and it has extra reproductive value whenever it survives alongside older siblings. Insurance reproductive value (RV_i) can be calculated as

$$RV_i = (1 - q) P_i, \quad (1)$$

and the extra reproductive value (RV_e) as

$$RV_e = q P_e, \quad (2)$$

where q is the proportion of broods in which the youngest egg/nestling is not predeceased by an older nestmate, P_e is the fraction of q in which the youngest survives, and P_i is the fraction of the $(1 - q)$ broods in which the youngest survives. RV_i can be further divided into two categories depending on whether the survival of the last chick is conditional on the death of an older nestmate (Lamey et al. unpubl. data), but I did not divide RV_i in order to compare my results with previous studies. I included only four- and five-egg clutches: (1) that were not part of posthatching experimental manipulations; and (2) for which the fate of the last egg/nestling was known.

Results.—Over the five years, there were 351 nesting attempts with sufficient information on the fate of eggs and nestlings to include in calculations of reproductive value (Table 1). The calculations were performed separately for each year because the number of prey (small mammals) showed significant annual variation. According to trap-line censuses conducted each year in July (the nesting period of kestrels), there were 8 small mammals per 100 traps in the poorest food-year (1990) and about 22 individuals per 100 traps in the best food-year (1988; Wiebe and Bortolotti 1992, 1994). Despite the variation in food supply, the proportion of broods in which the last-hatched nestling survived (RV_{tot}) was similar across years ($\bar{x} = 0.68 \pm \text{SD of } 0.03$). Likewise, the parameters used to calculate reproductive values of the last-hatched nestling had little annual variation (Table 1). Most of the reproductive value of the last nestling was extra value, but 35% of the total reproductive value was insurance, with the last young replacing an older egg or sibling that had died.

I calculated the reproductive values of last-hatched nestlings separately for the two most common clutch sizes (95% combined) of American Kestrels: four eggs

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TABLE 1. Insurance reproductive value (RV_i) and extra reproductive value (RV_e) of the last-laid egg in American Kestrel clutches from 1988 to 1992, with data on clutches of four and five combined.* Sample size refers to number of broods used in calculations.

Year	<i>n</i>	<i>q</i>	(1 - <i>q</i>)	<i>P_e</i>	<i>P_i</i>	RV_i	RV_e	RV_{tot}
1988	44	0.73	0.27	0.59	0.75	0.20	0.43	0.63
1989	67	0.70	0.30	0.66	0.80	0.24	0.46	0.70
1990	78	0.74	0.26	0.62	0.70	0.25	0.46	0.71
1991	54	0.65	0.35	0.66	0.78	0.27	0.43	0.70
1992	108	0.64	0.36	0.64	0.70	0.25	0.41	0.66
\bar{x}	351	0.69	0.31	0.63	0.75	0.24	0.44	0.68

* See Methods for definitions of *q*, *P_e*, and *P_i*. $RV_{tot} = RV_i + RV_e$.

(*n* = 67 clutches); and five eggs (*n* = 284 clutches). While the absolute value and apportionment of reproductive value has been shown to vary with clutch size for several species (Table 2), such was not the case for American Kestrels. In general, the insurance role of kestrel nestlings was as large as found in some species with obligate brood reduction in which insurance was the only form of reproductive value (Table 2). RV_i was relatively large for kestrels because many clutches had hatching problems. Among nests where at least one egg hatched (*n* = 493), 34% had some hatching failure. The majority of nests with partial hatching failure contained infertile eggs or embryos dying before term (Fig. 1; see also Wiebe and Bortolotti 1995b). Blood spots can be detected in kestrel eggs after 48 h of incubation (Bird et al. 1984), but it is possible that few very early embryo deaths

would have been classified as "infertility." Other causes of failure were eggs disappearing (presumably taken by predators such as squirrels), eggs damaged during incubation, chicks dying while hatching, and capping of an egg during hatching by a previously hatched egg.

Discussion.—Birds apparently hatch more young than they normally raise for three main reasons, none of which are mutually exclusive: resource tracking, insurance, and sib facilitation (e.g. food storage; see Mock and Forbes 1995). According to the resource-tracking hypothesis, surplus offspring serve to match brood size to a variable and unpredictable food supply. Periods of bad weather during which kestrels are unable to forage can make hunting success unpredictable, and asynchrony in kestrel broods facilitates the death of the youngest nestling if food is scarce for the brood (Wiebe and Bortolotti 1995a). Thus, the youngest kestrel nestlings in a brood have a large resource-tracking function (RV_e ; Table 1).

Because there were infertility and hatching problems in a large percentage of kestrel clutches, last-hatched nestlings also played a second, significant role as insurance (RV_i), replacing older siblings. Others studying American Kestrels typically have reported high rates of egg failure (between 20–45% of eggs laid; see review in Bird 1988), although Balgooyen (1976) found nearly 100% hatching success in his population. Young kestrel nestlings also played a third role as a living larder for older siblings once food became scarce (the "icebox" hypothesis; Alexander 1974). Parents and siblings cannibalized dead nestlings, but only 20 to 63% of carcasses were eaten

TABLE 2. Comparison of reproductive value of last-hatched nestlings of several species. Species arranged in order of increasing reproductive value.

Species	Clutch size	RV_i	RV_e	RV_{tot}	Source
Obligate brood reduction					
<i>Eudypetes chrysolophus</i>	2	0.11	0	0.11	Williams (1980)
<i>Sula dactylatra</i>	2	0.20	0	0.20	Kepler (1969)
					Anderson (1989)
<i>Pelecanus erythrorhynchos</i>	2	0.20	0	0.20	Cash and Evans (1986)
<i>Aquila verreauxi</i>	2	0.23	0	0.23	Gargett (1977)
Facultative brood reduction					
<i>Rissa tridactyla</i>	2	0.09	0.31	0.40	Braun and Hunt (1983)
<i>Forpus passerinus</i>	5–6	0.43	0.15	0.58	Beissinger and Waltman (1991)
	7–8	0.27	0.17	0.44	
<i>Casmerodius albus</i>	3	0.48	0.15	0.63	Mock and Parker (1986)
	4	0	0.23	0.23	
<i>Sula neboxii</i>	2	0.05	0.67	0.72	Drummond, cited in Mock et al. (1990)
	3	0.05	0.06	0.11	
<i>Ardea herodias</i>	3	0.14	0.05	0.19	Mock and Parker (1986)
	4	0	0.68	0.68	
<i>Falco sparverius</i>	4	0.28	0.44	0.72	This study
	5	0.26	0.43	0.69	
<i>Pandion haliaetus</i>	2	0	0.71	0.71	Stinson (1977)
	3	0	0.83	0.83	

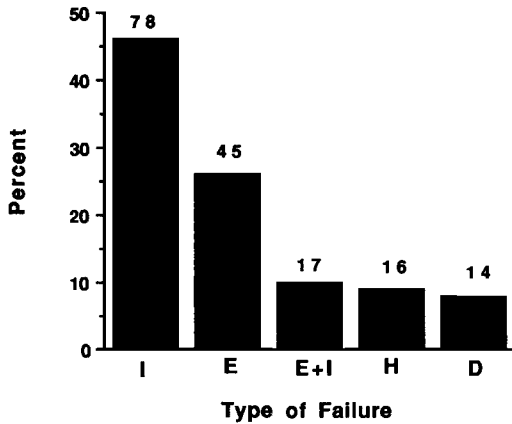


Fig. 1. Causes of partial hatching failure in American Kestrel clutches (n above bar). Sample is 170 nests in which some failure occurred. Types of failure: (I) infertile egg; (E) embryo died before hatching; (H) chick died while hatching; (D) egg disappeared or damaged. Clutch sizes four and five from 1988 to 1992 combined.

annually, depending on small-mammal abundance on the territory (Bortolotti et al. 1991). The food value of kestrel carcasses is probably a small side benefit of brood reduction rather than the main cause for hatching and raising surplus young. However, dead nestlings may provide a small meal at a critical time.

Within a species, the survival of the last-hatched young may vary according to food supply, clutch size, or age of the parents. For example, life-history theory suggests that parents may be willing to invest more in their offspring at the end of their reproductive life, leading to a higher RV_e for nestlings of older parents (Mock and Parker in press). RV_e might decrease with age or experience as parents become more proficient at hatching or guarding eggs. I was unable to age kestrels with certainty, but the reproductive value of last nestlings did not change with annual variation in food supply (Table 1). This suggests that parents have some ability to predict food abundance among years (see Wiebe in press) and to adjust reproductive parameters such as sex ratio (Wiebe and Bortolotti 1992) and hatching asynchrony (Wiebe and Bortolotti 1994) to match the energy demand of the brood to food supply. Thus, kestrel clutches may vary in terms of total energy demand on parents, but each clutch might be individually optimized to have, relatively speaking, the same insurance and resource-tracking functions. Kestrel parents, in contrast to those species like Great Egrets (*Casmerodius albus*) and Blue-footed Boobies (*Sula nebouxi*) that are listed in Table 2, also seem to adjust provisioning effort to clutch size so that last nestlings in broods of four and five received proportionately the same investment.

Whether or not to lay surplus eggs depends on a variety of costs and benefits. Insurance offspring are most valuable when: (1) the rate of offspring failure is high; (2) clutch size is large; (3) the cost of offspring formation is small; and (4) there is a mechanism for removing surplus offspring (Forbes 1990). With some form of hatching failure occurring in about 34% of nests, the benefits of insurance offspring seem clear. American Kestrels lay relatively large eggs for their body size (see Newton 1979), but can lay more eggs within days if their first clutch is accidentally destroyed (pers. obs.). Although the short- and long-term costs of egg formation are not known, parents can recoup some of these energy costs when they cannibalize the dead offspring. We rarely observed direct physical aggression within kestrel broods, but competitive asymmetries resulting from hatching asynchrony probably kept the cost of terminating surplus offspring low (see Wiebe and Bortolotti 1995a). An unusual cost of surplus offspring for kestrels may be at the incubation stage. A small body size relative to egg size and a peculiar arrangement of brood patches may limit the number of eggs that can be incubated effectively (Wiebe and Bortolotti 1993). Even with a five-egg clutch, the modal clutch size of kestrels, hatching failures were higher for small-bodied females (Bortolotti and Wiebe 1993).

Last-hatched young within American Kestrel broods provide benefits to parents (and siblings) in each of the three classes summarized by Mock and Forbes (1995), which is the first such documentation for any species of bird. Most of this benefit is in the form of extra reproductive value, but nestlings also act as insurance, and may play a small role as a larder. Quantifying costs and benefits of "extra" offspring at different stages of breeding and during different environmental conditions remain important questions for kestrels and other species with facultative brood reduction.

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