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AN EXPERIMENTAL STUDY OF THE COSTS OF REPRODUCTION IN THE KITTIWAKE RISSA TRIDACTYLA*: COMMENT*

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The cost of reproduction is a central concept in life history theory, encompassing any reduction in future survival or fecundity caused by a reproductive event (Roff 1992, Stearns 1992). The cost of reproduction has been measured by a variety of techniques, some of which have been criticized (Reznick 1985, 1992). One technique, phenotype manipulation (including clutch size manipulation), has been successfully used to demonstrate costs of reproduction in natural populations (Gustaffson and Sutherland 1988, Nur 1988, Møller 1993).

If the costs of reproduction are expressed as reduced survival, then accurate survival estimates of adults are required to show such costs. Unfortunately, in several cases, the evidence of decreased survival caused by high reproductive effort is based on improper survival estimates (see Pollock et al. 1990, Lebreton et al. 1992, 1993, Clobert 1995, Kendall and Nichols 1995, and Martin et al. 1995 for recent reviews). Jacobsen et al. (1995) recently reported experimental results on the costs of reproduction. In their experiment on Kittiwakes (*Rissa tridactyla*), clutch size was manipulated and adult survival responses were reported. Observing higher return rates for females in the reduced-brood group than for those in the control and enlarged-brood groups, Jacobsen et al. (1995) suggested that an increase of one offspring represented a significant increase in parental reproductive effort and, thus, resulted in a lower probability of survival to the subsequent season. However, considering the methods used to estimate survival probabilities and some other issues related to the experimental manipulation of brood size, we believe that alternative interpretations can be given. This weakens the authors' claim that their results provide evidence of a direct survival cost of reproduction in the Kittiwake.

The recapture or resighting at time $t + 1$ of an animal marked at time t depends on three events and their associated probabilities: the probability of surviving from time t to time $t + 1$ (i.e., the survival rate s); the probability, if alive, of being present in the studied area in year $t + 1$ (i.e., the presence probability m); and the probability that, if alive and present, the individual will be caught or resighted (i.e., the recapture or resighting probability p). In studies of a single population, only survival and recapture probabilities can be estimated separately. The presence probability is combined with either the survival (Clobert and Lebreton 1991) or recapture probability (Clobert et al. 1994, Kendall et al. 1995), depending on whether or not breeding dispersal is regarded as permanent. Although statistical methods to estimate each of these two quantities are now available (Pollock et al. 1990, Lebreton et al. 1992, 1993, Nichols 1992), most studies only report a compound estimate of survival and capture probabilities, i.e., the return rate (Clobert 1995, Martin et al. 1995). When return rates are compared between groups of individuals, any difference could be attributed to differences in either recapture, presence, or survival probabilities.

How are survival and recapture probabilities affected by costs of current reproduction? The answer depends on the type of short-term costs (see Clobert 1995). The cost may be paid by the individual as having either a higher probability of dying before the following reproductive opportunity (survival cost), or a higher probability of permanent dispersal (permanent dispersal cost). Either of these will result in a decrease in the survival probability. Alternatively, if the cost is expressed as reduced fecundity (either a higher probability of skipping one year of reproduction, or a lower probability of successfully rearing offspring, which may reduce presence in the breeding colony), or by temporary dispersal (attempted breeding elsewhere in a colony not studied), then the resighting or recapture probability decreases (Viallefont et al. 1995). The problem becomes more complex when long-term costs are considered, but statistical methods exist for dealing with such effects (see Nichols et al. 1994 and Clobert 1995 for review). An experimental protocol itself may influence subsequent tendencies to disperse or attempt reproduction. This is notably the case if the experimental manipulation affects reproductive success, which may, in turn, affect presence and recapture (resighting) probabilities if some failed breeders disperse or do not breed in the next year.

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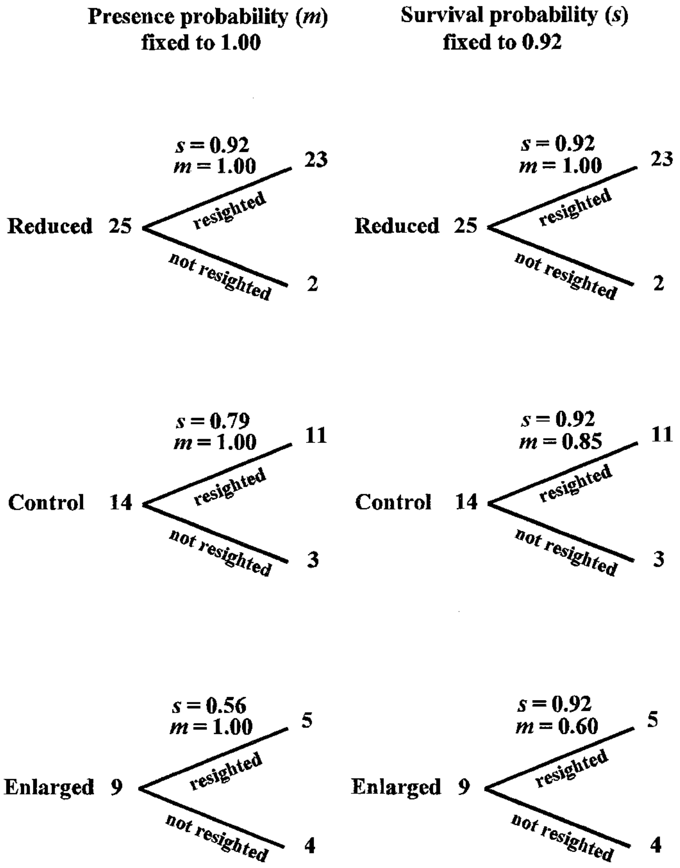

FIG. 1. Capture–recapture trees under various assumptions about survival (*s*) and presence (*m*) probabilities (recapture or resighting probability within the study plots is set to 1 in all cases). Reduced, Control, and Enlarged refer to brood size manipulation. Numbers refer to the number of birds in each experimental group of Jacobsen et al. (1995).

The experimental study recently reported by Jacobsen et al. (1995) illustrates the danger of ignoring capture and presence probabilities when inferring survival costs. In their study, Kittiwake brood sizes were experimentally increased or decreased. Return rates of experimental groups were compared to a control group. Females with enlarged broods had a significantly lower return rate (55.6%) than controls (78.6%) or females with reduced broods (92.0%) (Jacobsen et al. 1995). These values are referred to as survival rates, which implies that presence and recapture probabilities are equal to 1.0 for all three groups of females. Another possible interpretation might be that survival and recapture rates are constant, but that presence probabilities differ among groups. Let us assume that the true survival rate is equal to the highest return rate the authors observed (92%) and is constant for the three groups. Let us also assume, for illustrative purposes, that the recapture probability within the study plots is $p = 1.0$ (an assumption that easily could be checked using capture–mark–recapture models, provided that the timing of resighting is known). The observed return rates could be explained by presence probabilities (*m*) of 1.0 for the reduced brood group, 0.85 for the control group, and 0.60 for the enlarged brood group (Fig. 1). Under the above assumptions, the proportion of individuals not recaptured that are still alive in the following year is equal to $s(1 - m)$. In practical terms, it could be that three of the four individuals never resighted from the enlarged group moved to another breeding site or failed to breed in the year following the experiment (Fig. 1).

The authors seem to be aware of this problem. Their argument is that ‘‘most parts of the Hornoy and nearby islands were carefully searched for banded Kittiwakes in the three following breeding seasons,’’ and they state that ‘‘it is unlikely that large numbers of Kittiwakes have remained undiscovered.’’ This is not convincing to us. Three individuals in a colony of 21 000 pairs correspond to 0.007% (3/42 000) of the population, and cannot be represented as ‘‘large numbers.’’ Our experience of monitoring color-banded Kittiwakes in particularly favorable situations in Brittany (France) since 1979 (Danchin 1987, Danchin and Monnat 1992, Cadiou et al. 1994) allows us to state that one would need a minimum of 10 visits/yr to a given sample of breeding sites to miss finding <0.1% of the breeders. Even though this represents a high precision, this would mean missing up to 42 color-banded breeders in a colony of 21 000 pairs. Assuming that a good observer would take at least a full day to check 2000 pairs, this would represent 105 d of work for a single observer to monitor the breeders of the Hornoy colony with a 0.1% precision. Whether this effort was used in searching for banded birds is not reported.

Moreover, an alternative mechanism may be proposed to explain differences in the recapture and presence rates of the three groups. Birds, and notably seabirds, are well known to be less faithful to their breeding site and less likely to breed following a breeding failure rather than a breeding success (Coulson 1966, Brooke 1978, Schieck and Hannon 1989, Thompson and Hale 1989, Weimerskirch 1990, Beletsky and Orians 1991, Bensch and Hasselquist 1991, Danchin and Monnat 1992, Desrochers and Magrath 1993). In the consistently successful breeding colony of Kittiwakes of North Shields, the few adults that moved to a different colony did so after a failed breeding attempt or a disturbance (Coulson and Nève 1992). In Brittany, where nearby breeding cliffs show dramatic differences in reproductive success, dispersal and nonbreeding were documented more often, notably following local breeding failures (Danchin and Monnat 1992; E. Danchin, T. Boulinier, and M. Massot, *unpublished manuscript*). It is likely that dispersing or nonbreeding birds have a lower probability of being resighted in a large colony, as at Hornoy (Clobert and Lebreton 1991; E. Cam, J. E. Hines, J.-Y. Monnat, J. D. Nichols, and E. Danchin, *unpublished manuscript*). One can infer from Jacobsen et al. (1995: Table 1) the percentage of breeding failures in the three groups: 58.3% of nest failures ($n = 24$) for the group with enlarged broods; 50% of the nest failures ($n = 18$) for the control group; and 30% of nest failures ($n = 31$) for the group with decreased brood size. Thus, whatever their cause (due to the brood manipulation or to a confounding factor such as predation), it is possible that breeding failures in the three experimental groups differentially affected their likelihood to either disperse or fail to breed. This, in turn, may have affected recapture and presence probabilities rather than survival rate.

In light of these considerations, we do not believe that the ‘‘survival cost’’ hypothesis should be favored over the ‘‘nonbreeding or dispersal’’ hypothesis. The experimental brood size manipulation or some confounding factor may have affected the fate of birds in the different groups in a way not detectable by the reported experimental design. More generally, the existence of reproductive costs may not necessarily imply a direct reduction of survival subsequent to a reproductive event. For example, reproductive costs might be expressed in behavioral, not physiological, modifications. Attempts to disperse may be costly in terms of decreased probability of securing a site and a mate, and breeding successfully at a new site. Subsequent to breeding dispersal attempts, nonbreeding has notably been reported in the Kittiwake (Fairweather and Coulson 1995; E. Danchin, T. Boulinier, and M. Massot, *unpublished manuscript*). We suggest not only that careful phenotype manipulations be used, but also that close monitoring of the behavior and fate of individuals is needed to identify the costs of reproduction in natural populations (Clobert 1995, Nichols and Kendall 1995).

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