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CHANGES IN KING PENGUIN BREEDING CYCLE IN RESPONSE TO FOOD AVAILABILITY[1]

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Abstract. From 1991 to 1996 we investigated how the breeding cycle of King Penguins *Aptenodytes patagonicus,* in a small colony at South Georgia, was affected by variation in food availability between years. During the first (1992) and third (1996) of the three successful cycles studied, food was plentiful, whereas food availability was lower during the second cycle (1994). We found (1) the duration of breeding was longer (455 days) in 1994 compared to 1992 (437 days) and 1996 (438 days), (2) fewer birds made late breeding attempts in 1994 (38%) than in 1992 (88%) and 1996 (70%), and (3) those birds that made late attempts laid their egg later in 1994 (mean 16 March) compared to 1992 (19 February) and 1996 (21 February). We conclude that the breeding timetable changed in response both to the reduced availability of food in 1994 and to the subsequent improved conditions in 1996. This suggests that annual versus biennial breeding in King Penguins is dependent on the availability of food and the condition of the birds.

Key words: Antarctica, King Penguin, life-history trade-off, prey abundance, seabird, state-dependent decision.

For most birds, the period from laying eggs to fledging chicks is completed within one calendar year and breeding takes place annually at the same time each year. Depending upon abiotic factors, food availability often varies seasonally, and it is adaptive for birds to time energy-demanding events, like breeding and molting, to periods of high availability of food (Lack 1968, Perrins 1970). Birds with long development of offspring may have breeding cycles that exceed one year. In these species, the typical pattern is breeding every two years in synchrony with seasons, with one exception: the King Penguin *Aptenodytes patagonicus.*

King Penguins, breeding on sub-Antarctic islands, feed pelagically in polar waters on myctophid fish which are more available in summer than in winter (Cherel et al. 1993, Olsson and North, in press). The breeding cycle, including prebreeding molt, takes 13–16 months to complete successfully (Weimerskirch et al. 1992, Jouventin and Lagarde 1995, Olsson 1996). The single chick overwinters in the colony and is rarely or never fed during this time. The parents resume provisioning the next spring (September–October) and the chick becomes independent some months later. Hence, a complete breeding and molt cycle, from one egg-laying to the next, involves two summers. Despite this, the parents then molt and may start a new breeding attempt the second of these two summers, that is the same summer as the previous chick fledged, but this time in February or March instead of in November or December, which was the start time of the previous breeding. Thus, they often try to breed each summer (annually) and there are typically two temporally separated peaks of breeding activities in a King Penguin colony, depending on the outcome of the previous attempt (for details, see Olsson 1996).

The general pattern of the King Penguin breeding cycle is similar in various locations, including South Georgia (Stonehouse 1960, Olsson 1996), Crozet Archipelago (Barrat 1976, Weimerskirch et al. 1992, Jouventin and Lagarde 1995), Heard Island (van den Hoff 1993), and Marion Island (du Plessis et al. 1994, van Heezik et al. 1994). Nevertheless, there are some differences in the timing of the late breeding attempts and the proportion of birds undertaking them. It is probable that such differences depend on food availability (Weimerskirch et al. 1992, Olsson 1996).

We investigated three breeding cycles which were temporally separated by years of total failure. In the first and last cycle, the availability of food was good, whereas it was lower during the intermediate cycle. We compared (1) the duration of the breeding cycle, (2) the proportion of successful birds preparing for (molt, courtship) or starting (egg laid) late breeding, and (3) the timing of egg-laying in late attempts. Compared to the first and last cycle, we expected to find significant changes in all three variables in the second cycle when food availability was lower.

METHODS

We studied a King Penguin colony (~200 individuals) at Husvik (54°11′S, 36°40′W), South Georgia each

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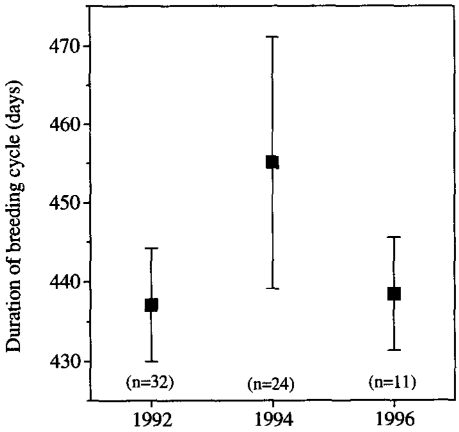

FIGURE 1. Mean ± SD duration of successful breeding cycles of King Penguins, i.e., from one egg-laying to the next.

austral summer from 1990/1991 to 1995/1996. The main study period each season was from October or November to March or April. For convenience, we will refer to the austral summers by the their last calendar year, e.g., the summer of 1991/1992 is 1992, etc. Moreover, the breeding cycle that started in the austral summer of 1990/1991 and ended in the 1991/1992 summer, will be referred to as the breeding cycle of 1992, because that is the summer of fledging.

Almost all birds in the colony were individually identified by using metal flipper bands and passive implanted electronic transponder tags (TIRIS). Transponders served as backup marking for potential band loss which, however, did not occur. We could read more than 95% of the bands daily with a telescope or binoculars.

Two observations supported the assumption that food availability was poor in the summer of 1994 relative to the other summers of this study. First, the duration of foraging trips was longer in 1994 (Olsson 1995), which suggests that birds were less able to find food. As a consequence, > 60% of pairs failed during incubation in 1994 compared to < 10% of failure during the other summers. Second, a larger proportion of otoliths from the main prey fish was eroded in 1994 (Olsson and North, in press), suggesting that prey were caught further away from the colony and/or less frequently. Moreover, the nutritional condition in general for higher predators around South Georgia was very poor in 1994 (Boyd et al. 1995, Brierley and Watkins 1996).

RESULTS

The successful breeding cycles of 1992, 1994, and 1996 resulted in 32, 33, and 10 fledging chicks, respectively. In the intervening summers, 1993 and 1995, no chicks fledged.

Measured from one egg-laying to the next, including molting, there was a significant difference in duration of breeding between the three successful breeding cycles (ANOVA, $F_{2,64} = 19.5$, $P < 0.001$). The 1994 cycle lasted on average 455 days (65 weeks) and was 18 and 17 days longer than the cycles of 1992 and 1996, respectively (Fig. 1).

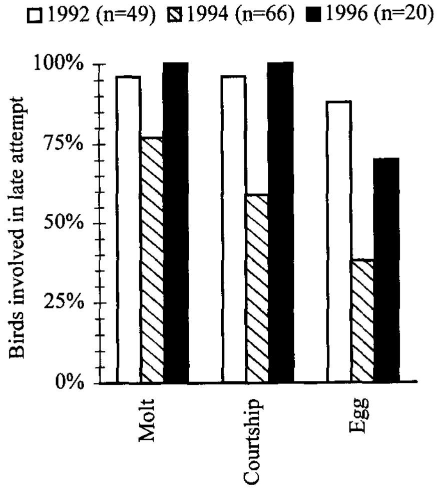

FIGURE 2. Percentage of King Penguins involved in preparations for late breeding attempts (prebreeding molt and courtship) and accomplishing late breeding attempts (egg laid), after having raised a chick to independence earlier the same summer.

There were no significant differences between the three breeding cycles in the proportion of birds starting a late prebreeding molt ($\chi^2_2 = 0.8$, $P = 0.66$) and late courtship ($\chi^2_2 = 4.2$, $P = 0.12$), after having raised a chick to independence (Fig. 2). There was, however, a significant difference between the three cycles in the proportion of birds that had a late egg. ($\chi^2_2 = 13.8$, $P = 0.001$) (Fig. 2). Although the difference was significant only for egg-laying, Figure 2 shows that the pattern also was the same for molt and courtship: high proportions of birds were involved in 1992 and in 1996, whereas lower proportions were involved in 1994.

The mean (± SD) dates of egg-laying for birds making late breeding attempts were similar in 1992 and in 1996; 19 February ± 11.3 days ($n = 26$) and 21 February ± 9.1 days ($n = 8$), respectively. In 1994, however, the mean date was later, 16 March ± 18.9 days ($n = 14$). This difference in mean laying date of late attempts between years was significant ($F_{2,45} = 17.2$, $P < 0.001$).

DISCUSSION

REASONS FOR BREEDING FAILURE IN 1993 AND 1995

The reason why no pair was successful in 1993 was likely some combination of: (1) a large proportion of the birds in the colony were successful in their previous attempt and hence were late breeders, which made them less likely to breed successfully (Weimerskirch et al. 1992, Jouventin and Lagarde 1995, Olsson 1996); (2) among the early breeders, which normally are more likely to be successful, there was probably an unusually high proportion of low quality birds (see

Olsson 1996), which are more likely to fail; (3) some condition(s) such as weather and/or prey abundance may have been particularly unfavorable during the winter of 1993; survival of chicks also was low in the larger Fortuna Bay colony approximately 15 km away (as it was in the winter of 1995). The reason for no chicks fledging in 1995 was the extremely poor foraging conditions in the summer of 1994. All pairs laying eggs failed before the winter and, hence, no chick was alive that could fledge in 1995.

It seems paradoxical that the poor summer of 1994 had no effect on prefledging survival of the over-wintered yearling chicks that hatched in 1993, whereas those chicks that hatched in 1994 all died before the winter. However, compared to over-wintered yearling chicks fledging in 1992, those fledging in 1994 weighed less prior to departure, fledged at a later date, and the survival and recruitment rates were lower (Olsson, in press b).

A consequence of the complete failure in 1993 and 1995 was that each of the three successful breeding cycles (1992, 1994, and 1996) were separated by a year of failure. This temporal separation also allowed us to compare seasons when all birds in the colony were early breeders, and therefore data were not confounded by different proportions of birds with presumably different prospects of breeding success, due to late breeding, in the three years compared.

EFFECTS OF POOR FOOD AVAILABILITY

Compared to the 1992 breeding cycle, when availability of food was good, the 1994 breeding cycle was longer, fewer birds made late attempts, and those that laid eggs did so later. Moreover, in 1996, when the availability of food was good again, the duration of the breeding cycle, the proportion of birds undertaking late attempts, and timing of late egg-laying all were similar to 1992. Hence, our predictions were supported and we conclude that the main features of the King Penguin breeding cycle are influenced by the availability of food.

We believe that the differences in 1994 are related to the fact that all activities which involved foraging took longer time in 1994. For example, the chicks were fed less often and therefore required longer time to fledge, which delayed the late breeding attempt of their parents. Also, fattening trips to sea to acquire reserves in preparation for prebreeding molt and courtship took longer time and caused further delay (Olsson 1995).

The fact that more birds refrained from late breeding attempts in the poor year of 1994 suggests that this is a decision which is influenced by the prospect of obtaining sufficient food for breeding, without increasing energy expenditure too much. At least four variables may be involved in the decision of whether to undertake a late breeding attempt or not: the date of fledging of the previous chick, prey availability, the general condition of the bird, such as fat reserves, and previous experience. Consequently, annual versus biennial breeding may be a decision which is dependent on the condition or "state" of the birds (see McNamara and Houston 1996). Similarly, state-dependent decisions also may influence clutch abandonment in King Penguins (Olsson, in press a).

A combination of three features makes the King Penguin breeding cycle unique: it exceeds one year, molt takes place before breeding, and they make a late breeding attempt after the first chick has fledged in the second summer. In all wild populations, over-wintering of the chick seems to be obligatory (Williams 1995). The reason for this may be that the alternative, the chick becoming independent at the end of the first summer, may result in reduced chick survival because the inexperienced chick has to learn to feed for itself at a time of year when food availability is declining rapidly. The late breeding attempts of successful birds, on the other hand, seem to be optional and flexible. We suggest its occurrence and timing can be greatly influenced by the availability of food. However, it remains unclear why late attempts are made at all, considering that very few such attempts are successful (Weimerskirch et al. 1992, van Heezik et al, 1994, Olsson 1996). The answer may be that breeding incurs only small extra costs compared to the potential advantages of success if availability of food is unusually good (Olsson 1996).

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THE LENGTH OF INCUBATION IN RELATION TO NEST INITIATION DATE AND CLUTCH SIZE IN DABBLING DUCKS[1]

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Abstract. There are a growing number of studies which suggest that variable incubation periods may be the norm for waterfowl, and that this variation may be correlated with other life-history traits. I examined variation in length of incubation in relation to nest initiation date and clutch size in five species of dabbling ducks during 1995 and 1996. I also conducted a manipulative experiment to directly assess the relationship between clutch size and incubation period in Blue-winged Teal (*Anas discors*). The length of incubation declined seasonally for all species and in both years. After controlling for nest initiation date, incubation periods were positively correlated with clutch size in only one species during one of two years. Enlarged clutches were incubated two days longer than control or reduced clutches, although reduced and control clutches had similar incubation lengths. These results suggest that clutch size explains only a small amount of the total variation in incubation length, and the cost of incubation may operate with other factors to help limit clutch size in Blue-winged Teal.

Key words: Blue-winged Teal, clutch size, Gadwall, incubation period, Mallard, nest initiation date, Northern Pintail, Northern Shoveler.

The length of incubation in waterfowl may have important consequences for individual fitness, including length of exposure to predators (Arnold et al. 1987) and parental energetics (Thompson and Raveling 1987). Whereas many studies have focused on interspecific variation in incubation periods (reviewed by Afton and Paulus 1992), relatively few studies have addressed intraspecific variation. In general, waterfowl incubation periods have been reported as single values. However, there are a growing number of studies which suggest that variable incubation periods may be the norm for waterfowl (Aldrich and Raveling 1983, Hepp et al. 1990, Arnold 1993). In addition, this variation may be correlated with other life-history traits. Hepp et al. (1990) showed that incubation periods in Wood Ducks (*Aix sponsa*) was positively correlated with clutch size (i.e., dump nests), and the length of incubation declined with nest initiation date in one of three years. Arnold (1993) found a similar seasonal decline in incubation period for artificially-incubated dabbling duck eggs (*Anas* spp.).

In this study, I examined the effect of nest initiation date and clutch size on the length of incubation in five species of upland nesting dabbling ducks: Blue-winged Teal (*Anas discors*), Mallards (*A. platyrhynchos*), Gadwalls (*A. strepera*), Northern Pintails (*A. acuta*), and Northern Shovelers (*A. clypeata*). In addition, I conducted a clutch size manipulation experiment to di-

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