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## **Male Incubation and its Effect on Reproductive Success in the Black Swan, *Cygnus atratus***

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### **Abstract**

Male incubation is very unusual among Anatidae. In the black swan, males spend more time incubating the clutch than females do. We investigated the incubation patterns of males and females in a breeding colony in Vienna over a one-year period. Breeding occurred year round, with a peak in winter. Inattentive periods during incubation were shorter in winter than at other times of the year, probably because the heat loss of eggs is then higher. We tested the importance of the costs of incubation by prolonging the breeding period experimentally. Eggs were exchanged for dummies, which were readily accepted and incubated for up to 342 days. The higher the incubation effort of females, measured as the product of their proportion of incubation and the total length of the incubation phase, the longer was the interval between the end of incubation and laying of a subsequent clutch. This suggests that the incubation effort of females is limiting the reproductive output of a pair. By taking charge of the greater part of incubation, males may increase the productivity of their female partners and thereby their own reproductive success. This amplification of female fecundity is a factor favouring a high share in male incubation which is discussed in polyandrous species (e.g. JENNI 1974) but generally overlooked in monogamous systems. The ultimate cause for male incubation in black swans may lie in the combination of a monogamous mating system and the capability of this species to breed whenever the environmental conditions turn favourable, at any time of the year.

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### **Introduction**

In most birds, males share in broodcare (LACK 1968). Apart from the importance of certainty in male paternity, three hypotheses are usually considered (MAYNARD SMITH 1984). A male share in broodcare would be favoured if (1) the effectiveness of parental care by two parents exceeds that of one parent at least twofold, (2) the chances of alternative mating are low, and (3) females are limited to provide sufficient broodcare by their effort of producing and laying a clutch.

Most attention has been given to post hatching care, but the participation of males in the early phases of broodcare (i.e. incubation) does not seem to be explained as easily within the framework of these hypotheses. As opposed to the stage when young are to be fed and/or protected, clutches can often be incubated as efficiently by one parent as by two (e.g. MARTIN et al. 1985; SCOTT 1984). The chances of alternative mating by a male should be relatively good early in the breeding cycle, and apart from extreme cases (e.g. kiwi, TABORSKY & TABORSKY 1993; M. TABORSKY, unpubl. data), females do not seem to be limited in their ability to incubate a clutch which they had just produced. Nevertheless, regular male participation in incubation occurs in 60 % of avian families (VAN TYNE & BERGER 1976). Its occurrence is variable in another 15 % (SKUTCH 1976). In the Anatidae, there are only very few species in which males take a regular share in incubation, despite the wide distribution of monogamy. They belong to four genera: *Anseranas (semipalmata)*, Anseranatinae, HAWKINS 1986; *Dendrocygna* (sp., Anserinae, HAWKINS 1986); *Thalassornis (leuconotus)*, Anatinae, KEAR 1970; *Cygnus* (*C. columbianus*, Anserinae: 13—39 % of incubation, EVANS 1977; SCOTT 1977; HAWKINS 1986; *C. bewickii*: 20—25 %, KONDRATIEV 1991; KRIVTSOV & MINEYEV 1991; *C. atratus*, MIERS & WILLIAMS 1969).

These anatids with a male share in incubation thus deviate from the general pattern of the family and are therefore especially well suited to study the functional significance of this behaviour. We investigated the share males take in incubation in the black swan (*Cygnus atratus*) to examine whether the three above mentioned hypotheses to account for male broodcare participation in general also suffice to explain male incubation.

Apart from being an exception to the rule, this species offers an additional advantage to investigate some of the questions regarding male participation in incubation. Black swans may breed all year round, depending on environmental conditions (BRAITHWAITE 1977). Therefore, the influence of climatic variation can be observed on the sharing of incubation tasks of males and females in a sort of “natural experiment”.

In this paper we show that males do not only participate in incubation, but incubate more than females do. “The evolution of predominant male care among monogamous birds is not well understood” (CLUTTON-BROCK 1991, p. 146). We tested the hypothesis that the reproductive rate of both, females and males, is limited by female incubation behaviour and that it may hence be increased by male participation. If this were true, our prediction was that males will take a greater share when the costs of incubation would be increased. Therefore, we raised parental effort by experimentally prolonging the natural incubation period through an exchange of eggs for dummies. Anatids generally accept dummy eggs and they often incubate non-developing eggs for periods greatly exceeding their natural incubation periods (SCOTT & The Wildfowl Trust 1972).

## Methods

Black swans (*Cygnus atratus*) originated from Australia. In contrast to other swan species they are non-territorial and breed in colonies. The start of nesting depends on rainfall (BRAITHWAITE 1977),

therefore black swans may breed at any time of the year (BRAITHWAITE 1982; WILLIAMS 1980). Some pairs even breed at temperatures well below 0 °C (STEINER, unpubl. data; own obs.).

We observed a free-living colony of black swans at the Wasserpark in Vienna (Austria), a standing water which was formerly an arm of the river Danube. The birds bred on an Island which is not accessible to people or other mammals, except for rats (*Rattus norvegicus*) and mice (*Mus musculus*). The population consisted of about 120–140 individuals at the start of our study, 99 of which were marked with numbered plastic neck collars. Water plants and algae were abundant and people fed the waterfowl at other locations in the park with supplementary food. Therefore, food was probably not limited at any time of the year. The behaviour of breeding males and females was recorded at and around the nest. From Sep. 1988 to Nov. 1989, we monitored the incubation patterns of all breeding pairs continuously by recording the presence of pair members at the nest and their activities (e.g. incubation, nest building, preening, egg turning, sleeping or sitting without any movement, etc.). For that purpose, observation scans were made each day for 1 or 2 h between 7.00 and 20.00 h, by aiming to obtain a complete record of one full daylight period in the course of each week. A total of 57 pairs at 116 nests were observed in this way. Pairs were recorded for an average period of 25 weeks.

We prolonged the natural incubation period of about 40 d in our population ( $\bar{x}$  = 40.8 d in mid winter:  $\bar{x}$  = 38.6 d in summer/autumn) experimentally by shaking eggs or exchanging them with plaster dummies.

### Analyses

When data distributions did not significantly differ from normality ( $p > 0.1$ ) we calculated arithmetic  $\bar{x}$  and SD; otherwise we computed medians and quartiles for confidence intervals and used nonparametric statistics (LIENERT 1973; SIEGEL 1987). Incubation data were grouped into 5-d intervals. We calculated  $\bar{x}$  and SD of the amount of male and female incubation behaviour for a period of 45 d (i.e. max. natural incubation period). We tested for differences between the male and female share in incubation with help of the Lord-test (LORD 1947). The first and second 5-d intervals were omitted from this analysis because incubation was often unstable during this period. The incubation effort of individual females was measured by multiplying the total length of their incubation period in days with their proportional share in incubation (i.e. net time for which the female was actually incubating). For a correlation analysis between this measure of female incubation effort and the interval to the subsequent clutch, we took the  $\bar{x}$  of both variables if a female was observed for more than one brood ( $n$  = 56 observations of 28 females).

For a comparison of inattentive periods (i.e. when eggs were not covered) between seasons we pooled the data for winter months, including Dec., Jan. and Feb.; for spring/autumn, including Apr., May and Oct.; and for summer: Jul., Aug. and Sep. Months in which only very few pairs incubated and the transitional months between seasons were omitted from this analysis. When data were grouped on a monthly basis to analyze the seasonality of incubation behaviour, the data of months in which pairs had started to incubate were excluded from the analysis for the reason given above (exclusion of the first and second 5-d intervals).

### Results

Black swans bred at all times of the year. Up to 30 pairs incubated simultaneously during the observation period, with a peak of clutch production in Jan./Feb. (Fig. 1) and a further increase during Aug. and Sep. ( $p < 0.001$ ,  $\chi^2$  test, difference from an equal distribution,  $n$  = 18). During this period we observed up to four breeding attempts per pair if the clutches did not succeed.

Within the maximum natural breeding period of 45 d, males took a greater share in incubation than females did (Fig. 2, 58 % versus 42 %;  $u$  = 0.959,  $p < 0.01$ , Lord-test,  $n$  = 7 male + 7 female 5-d periods; results from 51 males and 51 females are included in this data set). The incubation pattern of individual

Fig. 1: Annual distribution of the total number of incubated nests per month (empty bars). Hatched portions: new nests in which incubation started in the respective month

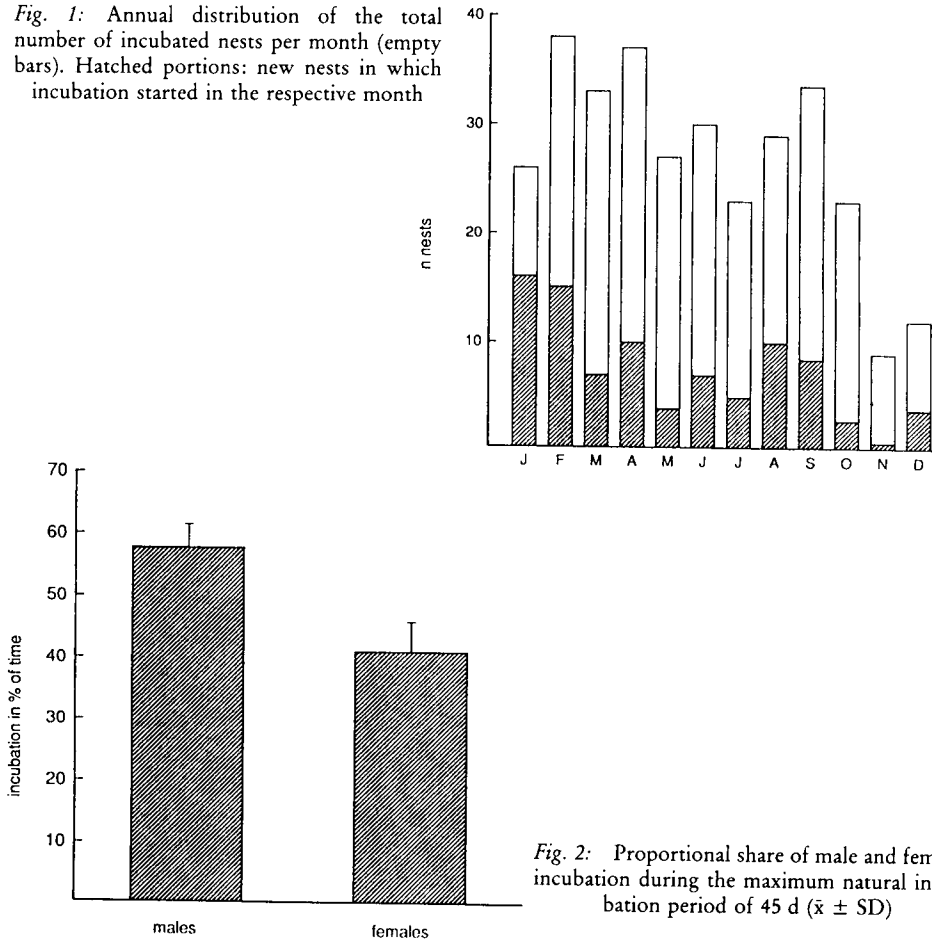
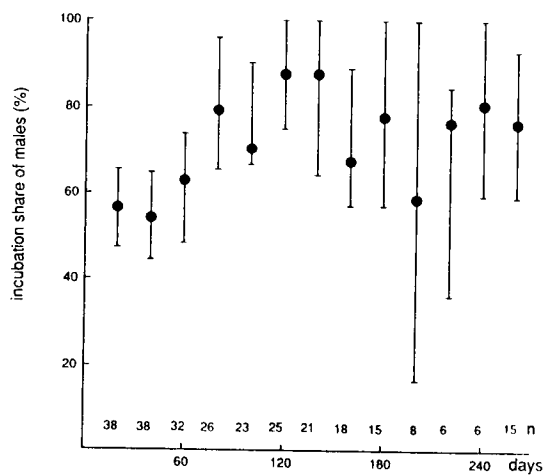


Fig. 2: Proportional share of male and female incubation during the maximum natural incubation period of 45 d ( $\bar{x} \pm SD$ )

Fig. 3: Experimentally prolonged incubation periods (max. 342 d) divided into 20-d sections. Dots: median values (with 95 % confidence intervals) of the males' incubation share, in %. The 13th to 17th 20-d periods were summarized, as the number of observations for each of these periods was below 6



males and females did not differ in successive clutches, but there were significant differences in the incubation share of males and females between breeding attempts of different pairs ( $p = 0.05$ , Kruskal-Wallis H-test,  $n = 22$ ). With an experimental prolongation of the incubation period the male's share of incubation increased to an average of 69.13 % (quartiles 55.72—82.40; difference from first 45 d was significant,  $p < 0.05$ , t-test,  $n = 37$ ). In a few cases females took over the majority of incubation at last, but in most cases males did (Fig. 3). By prolonging incubation we tested the amount of female incubation (independent variable) during the first clutch against the time it takes until females are able to lay the next clutch (dependent variable). The higher the incubation effort of females, the longer was the interval between the end of incubation of a clutch and laying of the next one (Fig. 4;  $r_s = 0.52$ ,  $p < 0.01$ , Spearman rank correlation analysis,  $n = \bar{x}$  of 28 females).

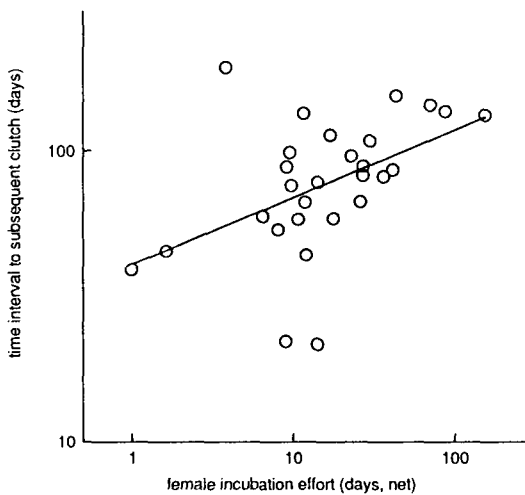


Fig. 4: Time intervals between end of incubation and subsequent laying, and incubation effort of females. The latter is the product of the total length of incubation in days and the proportional share the individual females took to incubate their eggs. Dots are  $\bar{x}$  of individual females. Both axes are log. scaled. X-values were transformed ( $x = x+1$ ) to permit log. scaling

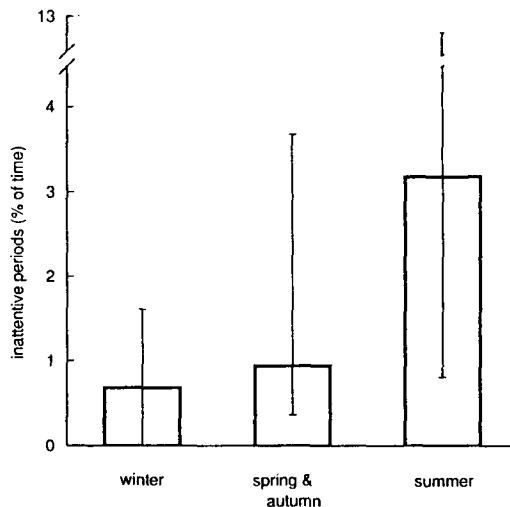


Fig. 5: Average lengths of inattentive periods of nests during the coldest (Dec., Jan., Feb.) moderate (Apr., May, Oct.) and warmest season (Jul., Aug., Sep.), measured in % of total time ( $\bar{x}$  and quartiles)

Incubation of eggs was almost continuous during daytime, apart from the early phases of incubation when eggs were uncovered for about 15 % of time on average. The lengths of incubation breaks were compared between the coldest, moderate and warmest seasons. Inattentive periods were longer in summer than in winter (Fig. 5  $p < 0.005$ , Mann-Whitney U-test,  $n_1 = 25$ ,  $n_2 = 26$ ), and there was a trend, albeit statistically not significant, that they were also longer in summer than in spring/autumn ( $p = 0.056$ , Mann-Whitney U-test,  $n_1 = 25$ ,  $n_2 = 34$ ).

We tested whether the proportional incubation share of males and females varied with clutch size. There was no relationship to be detected, neither with natural nor with experimental clutch sizes ( $p > 0.1$ , Spearman rank correlation analyses,  $n = 52$  and  $55$ ).

### Discussion

The Vienna population of black swans showed breeding peaks in Jan./Feb. like in Australia, even though the seasons are antithetic. KIKKAWA & YAMASHINA (1967) reported that black swans introduced to Japan bred there during the coldest months, too.

Male black swans performed more incubation than females did. This difference increased when the incubation period was experimentally prolonged with the help of egg dummies. By this manipulation we aimed at testing the hypotheses that (1) female productivity (i.e. reproductive rate) is limited by incubation, (2) males would compensate increased incubation costs to females by accepting a greater share of incubation, and (3) males could thereby raise their partner's and consequently their own reproductive success. We expected that a higher male share would reduce the time interval between successive clutches. The results show that the incubation effort of females is a limiting factor with regard to the reproductive output of a pair. Clutches can be produced year round in favourable conditions, and the intervals between them depend apparently on the female's previous incubation effort. Males can raise the reproductive rate of their partners by taking over the greater share of incubation. This increases their own reproductive success also, as the mating system of swans is monogamous and based on long term pair bonds (SCOTT & The Wildfowl Trust 1972; MARCHANT & HIGGINS 1990).

In wild whistling swans (*Cygnus columbianus*) females incubate for 81.3 % of time and males for 15.9 % (SCOTT 1977). HAWKINS (1986) found that only *female* whistling swans provide full incubation, however, because males do not have a brood patch and do not settle down on the eggs, therefore they only decelerate the cooling rate of the clutch. Neither female nor male black swans do have a brood patch. As males take over more than half of the incubation effort it is very unlikely that they do not fully incubate the clutch. Egg temperature measurements during incubation confirm that males fully incubate the eggs (C. BRUGGER, unpubl. data).

Biparental incubation enables a higher incubation constancy which results in a shorter incubation period and an increased protection of eggs from predators. It also allows incubating parents to leave the nest intermittently and for prolonged

periods of time to feed and thereby to compensate for their energy expenses. In the whooper (*Cygnus cygnus*) and probably most other northern swans in which females are the sole incubators the latter leave their nests only to feed for about ½ h daily, during the warmest part of the day. Incubating mute swan (*Cygnus olor*) females are more irregular in their feeding patterns (BEEKMAN 1991), and so are the black-necked swans (*Cygnus melanocoryphus*). Both do not leave the nest more than once in every two or three days, mostly in the evening (SCOTT & The Wildfowl Trust 1972). Whistling swan females primarily feed before the start of incubation and while their mates construct and guard the nests (HAWKINS 1986). The northern swans always cover their eggs well with vegetation before leaving the nest, probably to slow down cooling, prevent dehydration and/or to protect the eggs from predators (SCOTT & The Wildfowl Trust 1972). Black swans do not cover the eggs when leaving the nest. Instead, they reduce the inattentive periods in colder conditions, probably to reduce the cooling of eggs. This is easily obtained by biparental incubation.

In conclusion, we believe that the three general hypotheses which are commonly involved to explain male participation in broodcare (see Introduction) do not sufficiently explain male incubation in black swans. Our data suggest that males can raise their partner's fecundity (and consequently their own reproductive success) by taking over the major share of incubation. This male effort may lead to a faster replenishment of female energy reserves and to a reduction of the interclutch time interval, at least if the present clutch fails and if the conditions for a new breeding attempt suddenly turn favourable. This is investment in future reproduction. These results contrast with evidence collected in an extensive comparative analysis by RIDLEY (1978), who concluded that there is no good evidence for enhanced female fecundity to be an evolutionary cause for paternal effort.

Two important conditions may have led to the probable causal link of an increase in female fecundity and the origin of male incubation in black swans. One is long term monogamy, i.e. incubating males may invest in their partners for their own future benefits. The other important feature is the unpredictable appearance of conditions enabling swans to start a new reproductive episode. The first condition is widespread in anatids (SCOTT & The Wildfowl Trust 1972; MARCHANT & HIGGINS 1990), but obviously not sufficient to lead to a male share in incubation. The second condition is rarely found in the ecology of members of this family, which usually depends on the regular fluctuations of a seasonal environment. This condition is probably the reason why male black swans deviate so much from their relatives in their participation in incubation duties. The importance of this condition has been anticipated by EMLEN & ORING (1977): "Males should assume the bulk of parental care . . . when the lack of dependability of breeding conditions places a premium on female ability to produce additional or replacement clutches for the male" (p. 220). They suggested that this may occur either when there are great fluctuations in the environmental suitability for breeding or very low success rates of reproductive attempts. Both conditions may apply for black swans (BRAITHWAITE 1981a, b). CLUTTON-BROCK (1991) argued that in such cases the advantage of rapid clutch replacement may

cause selection on both sexes to favour male care, but he had not found convincing evidence to support this explanation (p. 146). A comparable influence of male investment on female fecundity is however found in monogamous arctic waders producing double clutches (see RIDLEY 1978) or in the mallee fowl (FRITH 1962).

Causality might also be turned the other way. In mammals, monogamy "is likely to evolve where males can substantially enhance the reproductive rate of their mates by assisting in caring for the offspring (CLUTTON-BROCK 1991, p. 260; see DUNBAR 1988). In Anatids, however, monogamy prevails and male incubation is a very exceptional feature. Therefore we regard monogamy as a cause or important prerequisite of male incubation in black swans rather than as its effect.

One might argue that we showed only that males speed up female egg production in cases of *unsuccessful* breeding. In the variable and unpredictable natural environment of this species this may however be a very important factor (BRAITHWAITE 1982). It also points to the fact that this explanation of male broodcare may be important for other, even strongly seasonal species which are subject to a high rate of clutch failures while having the ability to produce replacement broods.

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### Literature Cited

- BEEKMAN, J. H. 1991: Laying date and clutch size in relation to body weight in the mute swan *Cygnus olor*. In: Proc. 3rd Int. Swan Symp. (SEARS, J. & BACON, P. J., eds.) Oxford, 1989; Wildfowl Spec. Suppl. No. 1, 279—287.
- BRAITHWAITE, L. W. 1977: Ecological studies of the black swan I. The egg, clutch and incubation; Aust. Wildl. Res. 4, 59—79.
- — 1981a: Ecological studies of the black swan II. Colour and plumage changes, growth rates, sexual maturation and timing and frequency of breeding; Aust. Wildl. Res. 8, 121—133.
- — 1981b: Ecological studies of the black swan III. Behaviour and social organization; Aust. Wildl. Res. 8, 135—146.
- — 1982: Ecological studies of the black swan IV. The timing and success of breeding on two nearby lakes on the southern tablelands of New South Wales; Aust. Wildl. Res. 9, 261—275.
- CLUTTON-BROCK, T. H. 1991: The Evolution of Parental Care. Princeton Univ. Press, Princeton.
- DUNBAR, R. I. M. 1988: Primate Social Systems. Croom Helm, London.
- EMLEN, S. T. & ORING, L. W. 1977: Ecology, sexual selection, and the evolution of mating systems. Science 197, 215—223.
- EVANS, M. E. 1977: Notes on the breeding behaviour of captive whistling swans. Wildfowl 28, 107—112.
- FRITH, H. J. 1962: The Mallee Fowl. Angus & Robertson, Sydney.
- HAWKINS, L. L. 1986: Nesting behaviour of male and female whistling swans and implications of male incubation. Wildfowl 37, 5—27.



- JENNI, D. A. 1974: Evolution of polyandry in birds. *Amer. Zool.* **14**, 129—144.
- KEAR, J. 1970: The adaptive radiation of parental care in waterfowl. In: *Social Behavior in Birds and Mammals*. (CROOK, J. H., ed.) Acad. Press, New York, pp. 357—392.
- KIKKAWA, J. & YAMASHINA, Y. 1967: Breeding of introduced black swans in Japan. *Emu* **66**, 377—381.
- KONDRATIEV, A. YA. 1991: Breeding biology of Bewick's swans *Cygnus bewickii* in Chukotka, Far Eastern USSR. In: *Proc. 3rd Int. Swan Symp.* (SEARS, J. & BACON, P. J., eds.) Oxford, 1989; *Wildfowl Spec. Suppl.* No. 1, 167—171.
- KRIVTSOV, S. K. & MINEYEV, YU. N. 1991: Daily time and energy budgets of whooper swans *Cygnus cygnus* and Bewick's swans *Cygnus bewickii* in the breeding season. In: *Proc. 3rd Int. Swan Symp.* (SEARS, J. & BACON, P. J., eds.) Oxford, 1989; *Wildfowl Spec. Suppl.* No. 1, 319—321.
- LACK, D. 1968: *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- LIENERT, G. A. 1973: *Verteilungsfreie Methoden in der Biostatistik*. 2. Aufl. Anton Hain Verl., Meisenheim am Glan.
- LORD, E. 1947: The use of the range in place of the standard deviation in the t-test. *Biometrika* **34**, 41—67.
- MARCHAND, S. M. & HIGGINS, P. J., eds. 1990: *Handbook of Australian, New Zealand and Antarctic Birds*. Vol. 1, Part B, Oxford Univ. Press, Melbourne.
- MARTIN, K., COOCH, F. G., ROCKWELL, R. F. & COOKE, F. 1985: Reproductive performance in lesser snow geese: are two parents essential? *Behav. Ecol. Sociobiol.* **17**, 257—263.
- MAYNARD SMITH, J. 1984: The ecology of sex. In: *Behavioural Ecology. An Evolutionary Approach*. (KREBS, J. R. & DAVIES, N. B., eds.) 2nd ed. Blackwell Sci. Publ., Oxford, pp. 201—221.
- MIERS, K. H. & WILLIAMS, M. 1969: Nesting of the black swan at Lake Ellesmere, New Zealand. *Wildfowl* **20**, 23—32.
- RIDLEY, M. 1978: Paternal care. *Animal Behav.* **26**, 904—932.
- SCOTT, D. 1977: Breeding behaviour of wild whistling swans. *Wildfowl* **28**, 101—106.
- — 1984: Parent-offspring association in mute swans (*Cygnus olor*). *Z. Tierpsychol.* **64**, 74—86.
- SCOTT, P. & The Wildfowl Trust 1972: *The Swans*. Michael Joseph, London.
- SIEGEL, S. 1987: *Nichtparametrische statistische Methoden*. Fachbuchhdlg. Psychol. Verlagsabt. Eschborn bei Frankfurt/Main.
- SKUTCH, A. F. 1976: *Parent Birds and their Young*. Univ. of Texas Press, Austin.
- TABORSKY, M. & TABORSKY, B. 1993: The kiwi's parental burden. *Nat. Hist.* **93** (12), 2—9.
- VAN TYNE, J. & BERGER, A. J. 1976: *Fundamentals of Ornithology*. 2nd ed. John Wiley, New York.
- WILLIAMS, M. 1980: The demography of New Zealand's *Cygnus atratus* population. *2nd Int. Swan Symp.*, Sapporo, 1980; *Wildl. Serv. Publ.* No. **242**, 147—160.

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