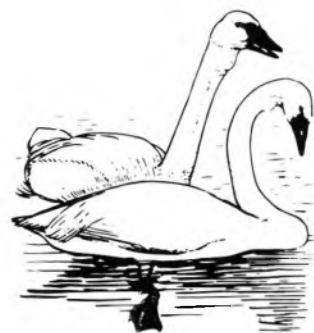# Division of labour in breeding Trumpeter Swans *Cygnus buccinator*

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*We used time budget analysis to quantify and compare breeding behaviour of male and female Trumpeter Swans nesting in Alaska (1988 and 1989) and in Idaho and Wyoming (1991). Females fed more than males during the prelaying/laying period while males provided the bulk of nest construction. Males spent more time at the nest during female incubation recesses and less time at the nest when females were incubating. Males were more alert and aggressive when incubating females left the nest, and they fed and slept less. Male nest-sitting, previously undescribed for wild Trumpeter Swans, was a regular behaviour for some males. All males were more active than females in repelling predators, and males were more aggressive toward other swans and geese. Male specialization in performing these duties probably enables females to accumulate or replenish nutrient and energy reserves more effectively and ultimately enhances the reproductive success of the pair.*

Monogamy is the predominant mating system in the Anserinae (Owen & Black 1990:66). Within monogamous pairs there is often a highly developed division of labour between the sexes (Lazarus & Inglis 1978, Sedinger & Raveling 1990, Gauthier & Tardif 1991). Females are preoccupied with feeding to build up or restore protein and lipid reserves, while males perform duties that allow their mates to maximise food intake. These duties include: (1) competition with conspecifics to acquire and maintain territories or feeding sites (Banko 1960, Kear 1972), (2) nest construction (Evans 1975), (3) attending mates or offspring during feeding bouts to discourage harassment by conspecifics (Stroud 1982, Gauthier & Tardif 1991), (4) guarding female, nest, and offspring from predators and nest parasites (Fox & Madsen 1981, Stroud 1982, Thompson & Raveling 1987, Madsen *et al.* 1989), and (5) sitting on eggs during female incubation recesses (Hawkins 1986).

Males provide these services because enhanced nutrient acquisition by the female results in reproductive benefits for both partners (Owen & Black 1990:38). Females that maximise nutrient intake prior to nesting lay larger clutches and have greater nesting success (Ankney & MacInnes 1978). Post-hatch females that restore depleted reserves are more likely to migrate successfully to wintering grounds and breed in future years (Sedinger & Raveling 1990). Mate-removal experiments show that males directly contribute to offspring survival (Schneider & Lamprecht 1990), and lifetime reproductive success in some swans is most strongly influenced by male characteristics rather than female traits (Scott 1988).

Male breeding behaviour is closely tied to proximate environmental conditions such as predation pressure, breeding densities and competition with conspecifics, climatic factors, and female energetic constraints. Tundra Swan *Cygnus columbianus columbianus* males, for example, sit on the eggs to protect them from predators when incubating females embark on feeding recesses, and a female feeds for longer periods if her mate sits on the nest (Hawkins 1986). In contrast, male Greenland White-fronted Geese *Anser albifrons flavirostris* accompany their mates during incubation recesses rather than guard the nest because benefits to females of feeding without harassment by conspecifics apparently outweigh the risks of predation (Stroud 1982).

Little quantitative research has been published on the breeding behaviour of wild Trumpeter Swans *Cygnus buccinator*. Trumpeter Swan females need to accumulate energy reserves before and after nest-

ing (Grant 1991), and they need to take frequent feeding recesses during incubation (Cooper 1979, Henson & Grant 1991). Male Trumpeter Swans, like most other Anserinae males (see above), probably perform duties that enhance their respective mates' forage intake. Our main objectives in this study were: (1) to describe important intersexual differences in Trumpeter Swan breeding behaviour, (2) to assess the respective influence of environmental factors and female energetic needs in determining male behaviour, and (3) to compare our results with what is known of other Anserinae. These objectives were achieved using time budget analysis to quantify the behaviour of male and female Trumpeter Swans during different stages of the breeding season.

## Methods

### Study areas

Trumpeter Swans were observed in 1988 and 1989 on the Copper River Delta, Alaska, and in 1991 in the Tristate Region of the Rocky Mountains (northwest Wyoming, southwest Montana, and southeast Idaho). The Copper River Delta is located adjacent to eastern Prince William Sound, Alaska, between $60^o$ and $60^o30'$N latitude and $144^oW$ longitude. Swans nested in ponds and lakes formed by glacial action or beaver *Castor canadensis* activity (Hansen *et al.* 1971), and important wetland macrophytes included the genera *Equisetum*, *Carex*, *Potamogeton*, *Hippuris*, *Sparganium*, and *Menyanthes*. Tristate swans were observed on wetlands in Yellowstone National Park, the Ashton and Island Park districts of the Targhee National Forest, Harriman State Park, and the Sand Creek State Wildlife Management Area. Other researchers have described the ecological aspects of this region in detail (Banko 1960, Shea 1979, Maj 1983). Important macrophytes for these wetlands included the genera *Nuphar*, *Carex*, *Potamogeton*, *Sparganium*, and *Eleocharis*.

### Field methods

Six nesting territories were selected for observation in 1988 and 1989 in Alaska (same territories both years), and six in

the Tristate Region in 1991. Territories and observation periods were not randomly selected due to logistical and access constraints. All portions of the diurnal period were regularly sampled, but the early-morning and late-evening hours were sampled less than the mid-morning to mid-afternoon hours. Nocturnal observations were conducted in the Tristate Region only and are detailed elsewhere (Henson 1991).

Observation blinds were built on scaffolding or nearby hills that overlooked nesting areas. All observation sites were hidden by vegetation and were located 100-293 m from the nest mounds. Observations were also conducted from vehicles parked on roads overlooking two territories. Field observers using telescopes conducted diurnal time budget observations at each territory every 2-4 days from the prelaying through the brood-rearing phases of reproduction. Observation periods averaged seven hours in length and ranged from four to 16 hours. Birds were sexed by observing copulations and egg-laying behaviours, and individuals were recognized by noting the unique feather stain patterns on the head and neck of each bird (Cooper 1979, Hawkins 1986). Additionally, neckbands were affixed to four Alaska birds in 1988. Age and breeding experience of individual birds were unknown, but all study wetlands have successfully produced Trumpeter Swan cygnets in the past (U.S. Fish and Wildlife Service unpubl. data).

Scan-observations (Altmann 1974) of swan locations and behaviour were recorded at 6-minute intervals with NEC-8300 (NEC Corporation, Tokyo, Japan) portable lap computers. (Grant (1991) found no difference in swan time budgets recording using 2-minute and 6-minute intervals, respectively.) Terminology describing incubation recesses, behaviour, and postures was adapted from Lazarus & Inglis (1978), Cooper (1979), and Hawkins (1986). Behaviour and locomotion categories included swimming, walking, flying, feeding, head-up, extreme head-up, preening, nest-building, courtship, agonistic interaction, sleeping or resting, incubation, and brooding. Rangefinders and compasses were used to ascribe location coordinates to each bird at each scan; these were entered into the programme with associated behav-

ioural observations. No visits to swan nests were made during the breeding season to minimize disturbance (Henson & Grant 1991), and laying, onset of incubation, and hatching dates were estimated from behavioural observations. Continuous observations (Altmann 1974) were made of short-duration behaviour such as territorial encounters, predator interactions, courtship, and responses to natural and human-caused disturbances. These observations were timed by stopwatch and described into a tape recorder.

## *Statistical analysis*

We combined results from Alaskan and Tristate birds into one data set because we

ues from 1988 and 1989 for three swan pairs that were known or suspected to occupy the same territories both years. Every individual bird thus contributed one mean value for each statistical test. This method decreased an already small sample size, but it is the most conservative approach. We used nonparametric methods for statistical comparisons (Zar 1984). Wilcoxon signed-rank tests were used to compare time budgets between paired males and females and for individual males under varying conditions (i.e. when females were incubating $v$ when females were on recess). Mann Whitney U-tests were used to measure intrasexual differences in behaviour between females and males with and without a brood.

**Table 1. Mean behavioural time budgets (%) for female (F) and male (M) Trumpeter Swans during separate periods of the breeding season. Rest for females includes sleep, rest, brood, and incubation.**

| Behaviour | Prelay/lay[a] | | Incubation[b] | | Post-hatch[c] | | No cygnets[d] | |
|---|---|---|---|---|---|---|---|---|
| | F | M | F | M | F | M | F | M |
| Feed | 48.1 * | 29.5 | 7.7 *** | 35.7 | 30.2† | 31.0 | 47.4† | 43.4 |
| Nestbuild | 11.0 * | 24.5 | 1.8 *** | 8.0 | 0.5 | 0.6† | 1.7 | 3.1† |
| Preen | 7.7 | 5.7 | 4.2 *** | 12.2 | 12.9 * | 15.7 | 15.2 | 18.2 |
| Rest | 12.4 | 16.6 | 81.2 *** | 11.9 | 28.4 ** | 13.9 | 14.4 | 12.7 |
| Head-up | 3.9 | 5.6 | 2.4 *** | 21.8 | 21.4 * | 28.2† | 15.8 | 16.1† |
| Ext. head-up | 1.2 | 2.0 | 1.7 *** | 7.5 | 1.3 * | 3.1 | 1.3 | 1.7 |
| Terr. Def. | 1.3 | 1.9 | 0.9 *** | 2.3 | 0.2 * | 0.6 | 0.1 | 0.7 |

[a]4 pairs; 1295 total observations.
[b]10 pairs; 11,429 total observations.
[c]9 pairs with cygnets; 2108 total observations.
[d]3 pairs without cygnets; 1890 total observations.
* = $P<0.005$, ** = $P<0.01$, *** = $P<0.005$, Wilcoxon test comparing time budgets between paired birds.
† = $P<0.05$, Mann Whitney U-test comparing within-sex time budgets between birds with and without cygnets.

are interested in gross differences in intersexual behaviour for this species. There were some differences in female incubation behaviour between birds from the two groups (Henson & Cooper in prep.), but overall behaviour patterns of the type described here did not differ between Alaskan and Tristate swans.

The breeding season was divided into prelaying/laying, incubation, and post-hatch periods. The number of observation days during the prelaying/laying period varied between territories and ranged from one to six days; territory establishment was observed for four swan pairs. A single estimate of activity for each incubation recess or observation day was calculated as the percentage of scans an individual spent in each behaviour during that recess or day. Overall mean values were calculated by averaging daily percentages for individual birds and then averaging individual means. We combined Alaska val-

## Results

Field workers studied 13 swan pairs (16 nest attempts) during 1704 hours of diurnal observation in 1988-91. Not all pairs were observed during each period of the breeding season due to access constraints, loss of eggs or brood, or abandonment of the observation territory.

### *Nesting behaviour*

Female swans fed more than males during the prelaying/laying period, while males spent more time than their mates nestbuilding (Table 1). Time budgets for all behaviours differed between the sexes during the incubation period (Table 1). Male swans spent more time at their nests ($\overline{x}$ = 55.4%, SE = 6.5) when females were on recess compared to when females were incubating (x = 30.2%, SE = 2.5) (Wilcoxon, $P$ = 0.008, $n$ = 10 males). Males were more

alert and aggressive when incubating females left the nest, and they fed and slept less (Table 2). Seven males sat on eggs 21 times during female incubation recess ($\bar{x}$ = 26.5 minutes, SE = 5.5); 14 of these sitting bouts occurred within one week of the start of incubation, two occurred during the three weeks of middle incubation, and five took place within one week of hatch. After hatch, females performed all brooding (defined as sheltering cygnets underwing) while males were more alert and territorial (Table 1). There were no significant intersexual behavioural differences for swans that lost their cygnets or failed to nest. However, females without cygnets spent more time feeding than females with cygnets, and males without cygnets spent less time alert and more time nest-building than males with cygnets (Table 1).

### Nest territory departures

Six swan pairs departed nesting wetlands together 20 times during the prelaying/laying period. Ten departures were feeding visits to nearby areas, while the purpose of the other ten was unknown. Pairs never left the nest area together once incubation had commenced except in brief agonistic encounters with other swans. Females left nest territories alone on 17 occasions during incubation ($\bar{x}$ length = 21.7 minutes, SE = 3.2). Two of these departures were feeding recesses, while the purpose of the others was unknown. Male swans always remained in attendance at the nest while females were gone. Males left the territories on 21 occasions, during which time females always remained on the nest.

### Predator interactions

Bald Eagles *Haliaeetus leucocephalus* were seen on swan nesting wetlands 24 times. Swans responded to the presence of eagles by becoming alert, calling, displaying, or giving chase. Males responded alone eight times, females once, and pairs responded jointly 15 times (13 of 15 times with males leading or becoming alert first). Eagles dived directly on cygnets or adults six times, and swans responded with hisses, spread wings, wing-flapping, and chase. A female swan gave the quivering-wings display (see Cooper 1979) to an eagle on one occasion. Two males chased eagles that were hunting ducklings even though direct threats to their cygnets were not made. All eagle predation attempts were not successful. Male swans also chased Common Ravens *Corvus corax* (*n* = 4), Black-billed Magpies *Pica pica* (*n* = 2), Arctic Terns *Sterna paradisaea* (*n* = 7), Osprey *Pandion haliaetus* (*n* = 2), and Belted Kingfishers *Megaceryle alcyon* (*n* = 1) that flew near or alighted on the nest. A male swan attempted to drive off a brown bear *Ursus arctos middendorffi* that attacked and destroyed a clutch in Alaska (see Henson & Grant (1992) for a detailed description). Swans sometimes displayed aggressively to non-predatory mammals such as beaver and moose *Alces alces*. Male swans chased moose away from the nest area four times, were alerted an additional ten times, and exhibited no reaction 13 times. Females never reacted aggressively to moose, but incubating females hid from moose on two occasions.

### Agonistic behaviour

Males of all study pairs spent more time than the females in territorial behaviour (Wilcoxon, *P* = 0.001, *n* = 13 pairs). Territorial behaviour for both sexes comprised less than 1% of the swans' overall time budgets due to the short duration of encounters. Intraspecific agonistic interactions ranged in length from ten seconds to 180 minutes ($\bar{x}$ = 17.4 minutes, SE = 5.1, *n* = 55), but 44% were under one minute in length. Nineteen (34.6%) of these confrontations involved direct physical contact or close displays with the intruding birds (birds within 1 m of one another), while the remainder consisted of vocalizations or displays to swans flying overhead (see Cooper (1979) for a description of typical displays). Intraspecific confrontations always involved both adults of the resident pair, and established resident birds won all encounters. Swans chased or displayed aggressively to other waterfowl species 121 times, with 101 (83.5%) interactions directed towards Canada Geese *Branta canadensis*; ducks were chased 20 times (16.5%). Interspecific interactions never involved both birds of a pair, and most took place while the female was incubating (76.1%). Males were responsible for 92.2% of the goose-chases, while males and females chased the same number of ducks.

One male swan chased a pair of American White Pelicans *Pelecanus erythrorhynchos* twice.

## Discussion

### Nest construction

Female Anserinae are concerned with maximizing food intake during the prelaying/laying period in order to accumulate nutrient reserves prior to egg laying (Owen & Black 1990:49). Presumably, the less time females spend in behaviours such as vigilance or nest construction during this critical period the more time they can devote to feeding. There were no intersexual differences in alert behaviour for Trumpeter Swans during this period, but males spent over twice as much time as females in nest-building behaviour. Evans (1977) observed a similar division of labour in captive Tundra Swans. In upland colonial geese, females tend to feed more than males during the prelaying/laying period while males spend more time vigilant for predators or conspecifics (Fox & Madsen 1981, Gauthier & Tardif 1991).

lower water but failed to nest.) Female Trumpeter Swans had previously been thought to provide most of the nest-building effort (Banko 1960, De Vos 1964, Cooper 1979).

### Male nest attendance

Most Anserinae females maintain high levels of incubation constancy to minimize the length of the incubation period and protect against egg predators (Aldrich & Raveling 1983, Madsen *et al.* 1989, Owen & Black 1990:53). However, many females need to take feeding recesses because energy reserves are depleted as incubation progresses (Thompson & Raveling 1987). This need for recesses must be reconciled with an increased risk of predation because birds that are least attentive to nests lose the most eggs to predators (Harvey 1971, Fox & Madsen 1981, Stroud 1982, Madsen *et al.* 1989, Sedinger & Raveling 1990). Predation of Trumpeter Swan eggs and cygnets is well-documented (Sharp 1951, Banko 1960, Hansen *et al.* 1971, Lumsden 1986, Henson & Grant 1992), and all males in this study performed nest-guarding duties. The male

**Table 2. Mean behavioural time budgets during the incubation period for male Trumpeter Swans while the female is away from the nest compared with while the female is on the nest.**

| Behaviour | Female off nest[a] x % | (SE) | Female on nest[b] x % | (SE) | P[c] |
|---|---|---|---|---|---|
| Feed | 8.4 | (1.8) | 29.3 | (2.3) | 0.003 |
| Nestbuild | 20.0 | (4.4) | 8.3 | (1.4) | 0.006 |
| Preen | 8.6 | (1.7) | 13.6 | (1.6) | 0.070 |
| Rest | 5.6 | (1.2) | 19.3 | (4.2) | 0.008 |
| Head-up | 29.1 | (3.8) | 18.3 | (1.7) | 0.011 |
| Ext. head-up | 22.2 | (4.4) | 7.02 | (1.3) | 0.003 |
| Terr. Def. | 5.4 | (1.9) | 2.3 | (0.2) | 0.006 |

[a]153 recesses observed, *n* = 898 total observations.
[b]*n* = 5789 total observations.
[c]Wilcoxon, *n* = 10 males.

There is relatively little need for Trumpeters to be vigilant for predators or conspecifics during this period because nesting territories are well-dispersed, conspecifics are scarce, and adult birds feeding on water are safe from predators (Banko 1960). Male energy is instead put towards construction of the nest, the large size of which provides insurance against flooding or egg predators (Hansen *et al.* 1971). (One study pair in Alaska failed to nest in 1989 because (we believed) its territory was flooded by beavers; the pair eventually moved to an adjacent area of

usually swam directly to the nest and assumed an alert posture as the female left the nest to feed. No eggs or cygnets were lost to avian predators in this study, a result that is more likely due to the vigorous attendance of males rather than to the absence of a serious predation threat. In addition to protecting their immediate reproductive interests (i.e. eggs), male swans may also be protecting their long-term interests (i.e. females). High levels of male nest attendance may allow females to feed for longer periods and increase the likelihood that they will end the

breeding season in good body condition (Schneider & Lamprecht 1990, Sedinger & Raveling 1990). Female Tundra Swans fed for longer periods when their mates sat on the nest (Hawkins 1986), but it is unknown whether female Trumpeter Swans would shorten incubation recesses or be less likely to feed if their mates provided little or no nest-guarding duties.

Male Trumpeters were also more alert than females after the eggs hatched. Presumably this allows females additional feeding time to replenish reserves prior to the rigours of autumn migration (Harwood 1977, Lazarus & Inglis 1978, Stroud 1982, Sedinger & Raveling 1990). We detected no differences in overall amounts of post-hatch feeding between males and females, but Grant (1991) found that Alaska females in this study fed 10-15% more than males during the ten days immediately after hatch.

*Male nest-sitting*

The males of five other swan species have been reported to sit on eggs during female recesses (Kear 1972), but the regular occurrence of male nest-sitting in wild Trumpeter Swans has not been described. Male nest-sitting is rare in captive Trumpeter Swans (De Vos 1964, Kear 1972, Cooper 1979) and until this study was not documented in the wild. Cooper (1979) proposed that bisexual incubation in swans minimizes the incubation period, aids in the protection of eggs from predators, and allows a higher level of feeding by the female during incubation. Hawkins (1986) concluded that well-developed male incubation behaviour in Tundra Swans was a protective response against egg predators but that it provided insulative benefits as well. She proposed that the behaviour was not essential for successful embryo development, but it may shorten the incubation by 6-7 days. Male nest-sitting in Trumpeter Swans is not as well developed as it is in Tundra Swans. Nest-sitting males did exhibit some of the nest-settling motions characteristic of incubating females (e.g. shifting of eggs and placement of feet beneath the eggs (see Cooper 1979)), but the behaviour was sporadic and was not correlated with the presence of predators or adverse weather (pers. obs.).

*Nest territory departures*

It is likely that all female territory departures during the prelaying/laying and incubation periods were feeding trips because all trips with observable destinations were to feeding grounds. Trumpeter males always accompanied females off the territories during prelaying/laying but failed to do so during incubation and instead remained by the nest. This temporal discrepancy in departure behaviour suggests that protection of the female or male paternity is paramount during prelaying/laying, while protection of the eggs is most important during incubation. Most male geese accompany their mates on prelaying/laying departures in order to protect the female from harassment by conspecifics or predators on the feeding grounds (Fox & Madsen 1981, Madsen *et al.* 1989), feed at better quality feeding grounds, or ensure their paternity by depriving females of extra-pair copulations. Extra-pair copulations have been reported for several species of monogamous geese (Mineau & Cooke 1979, Stroud 1982, Ely 1989, Lank *et al.* 1989, Welsh & Sedinger 1990, Gauthier & Tardif 1991) but to our knowledge have not been observed in swans.

*Agonistic behaviour*

As with nest construction and predator protection, males probably assume the responsibility for territorial defense because females are preoccupied with feeding or incubation (Evans 1975, 1977, Akesson & Raveling 1982, Madsen *et al.* 1989). Both members of a pair participate in intraspecific defenses, but only one bird at a time (usually the male) attacks other waterfowl. The reasons for this aggression are unclear. Banko (1960) reported that Trumpeter Swans tolerated ducks but were intolerant of larger birds. Our results generally agree with this observation, but some swans did chase ducks and ducklings. Individual variation in agonistic behaviour was pronounced, and male swans sometimes chased a particular goose even though other geese were on the wetlands and remained unmolested. Livezey & Humphrey (1985) proposed that much of the interspecific aggression in South American steamerducks may be a suite of secondary adapta-

tions for protection of the young, defense of food resources against marginal competitors, sexually-selected ritualized behaviour for assessment of males by females, combat practice, and non-adaptive "inertial" aggression. Trumpeter Swan aggression towards geese and ducks is consistent with all of these categories, particularly inertial aggression, and may be the result of similar conditions. Male swans often chased geese immediately after returning to the nest wetland from encounters with conspecifics; prior to such encounters these geese were tolerated. There were no obvious reasons for this agonistic behaviour because food was not limiting (Grant 1991) and geese were not a threat to swan broods (pers. obs.)

## Conclusions

Enhanced nutrient acquisition by female Anserinae results in higher productivity (Owen & Black 1990:38) and, theoretically, greater lifetime reproductive success for pairs (see Scott 1988). Our observations suggest that male Trumpeter Swans specialize in nest construction, vigilance and anti-predator behaviour, and territorial defense. This division of labour decreases the female's need to engage in nest-building and vigilance behaviours and probably allows her to accumulate or replenish reserves more effectively. This in turn increases reproductive success and makes long-term monogamy necessary in northern-breeding waterfowl with precocial offspring (Sedinger & Raveling 1990, Gauthier & Tardif 1991). It is likely that Trumpeter females without an attendant male would have lower reproductive success than would pairs, but this question needs to be addressed experimentally (see Martin *et al.* 1985, Schneider & Lamprecht 1990).

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