

4 *Long-term monogamy in a river specialist—the Blue Duck*

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Introduction

The mallard-sized Blue Duck *Hymenolaimus malacorhynchos*, endemic to New Zealand, is found mostly on rivers of steep gradient, a distinctive and linear habitat subjected to brief and dramatic changes in flow at any time of year. Adult ducks live year-round as pairs confined to exclusive 0.5–1.5 km territories along the river bed. Only territory-holders attempt breeding. Pairs keep close company at all times, males regularly patrol the territory boundaries, and territory (and mate) ownership are subjected to frequent challenges. Field and laboratory studies have yielded no evidence of mate infidelity nor of any breeding relationship other than strict monogamy (Triggs *et al.* 1991; Williams 1991). Males and females both care for the ducklings until fledging, that parental care consisting primarily of vigilance by the male and close guarding of the ducklings by the female. Both sexes are highly philopatric and birds resident in one catchment are effectively separate from those adjacent.

This appraisal of the Blue Duck mating system concentrates on the reproductive histories of 46 pairings over 14 breeding seasons (95 pair-years) during which 119 ducklings were fledged. From an analysis of pair characteristics and partner histories and reproductive success, we seek to appraise why long-term monogamy is characteristic of this species and other river-dwelling ducks, identify some of the costs and benefits of that system to individuals, and briefly summarize the nature of pair relationships in other ducks.

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Background, study site, and procedures

The Manganuiateao River in central North Island, New Zealand (see Fig. 4.1) is probably more typical of the bird's former and prime habitat than most areas in which it presently occurs. The study area extends over 9.3 km of river at the lower extremity of the bird's range on the river and at an elevation of 240–360 m. Blue Ducks occur on a further 30 km of the river up to an elevation of about 1000 m. Comparative demographic data from four more elevated and generally colder locations elsewhere in New Zealand indicate that within the Manganuiateao River study area Blue Ducks live longer, have smaller territories, are consistently more productive, and are more diurnally active.

In 1975 a volcanic lahar travelled down much of the Manganuiateao River rendering the entire study area (as well as a considerable area above it) uninhabitable by Blue Ducks. Although some of the displaced birds lived for a time in side streams, most then resident simply disappeared. This study commenced in the austral summer of 1980 with four pairs beginning the process of recolonization, and data up to and including the 1993 breeding season are included in the analyses. Most data were obtained during brief 3–4 day visits to the area approximately eight times annually. All resident adults and almost all of their progeny were caught and banded with unique combinations of colour bands. See Williams (1991) for details.

The mean clutch size was six eggs. Annual productivity after a 70–82 day fledging period was 1.3 young per breeding pair. Annual survival of breeders was 0.86 (male 0.92, female 0.80) and that of juveniles in their first year 0.44. Mortality, particularly of nesting females, resulted mostly from mammalian predation. Juveniles dispersed and established permanent residency within a few months of fledging and although some wandered extensively throughout, and possibly beyond, the natal catchment, both sexes were highly philopatric and sought to establish territories close to or within their natal range.

Although most territory-holding Blue Ducks nested each year, only about half successfully raised ducklings. Hence, the reproductive values are heavily skewed with zeros. A logistic regression analysis was performed, thus controlling for the Poisson distribution of the data. The dependent variables, when significant, such as male age and female age, were included in the models. Variation in reproductive success due to year (between 1980 and 1993) were also included in the analyses.

Results

The pair bond

The mating system in Blue Ducks was one of strict social monogamy. In all 87 confirmed breeding attempts territories and nests were defended

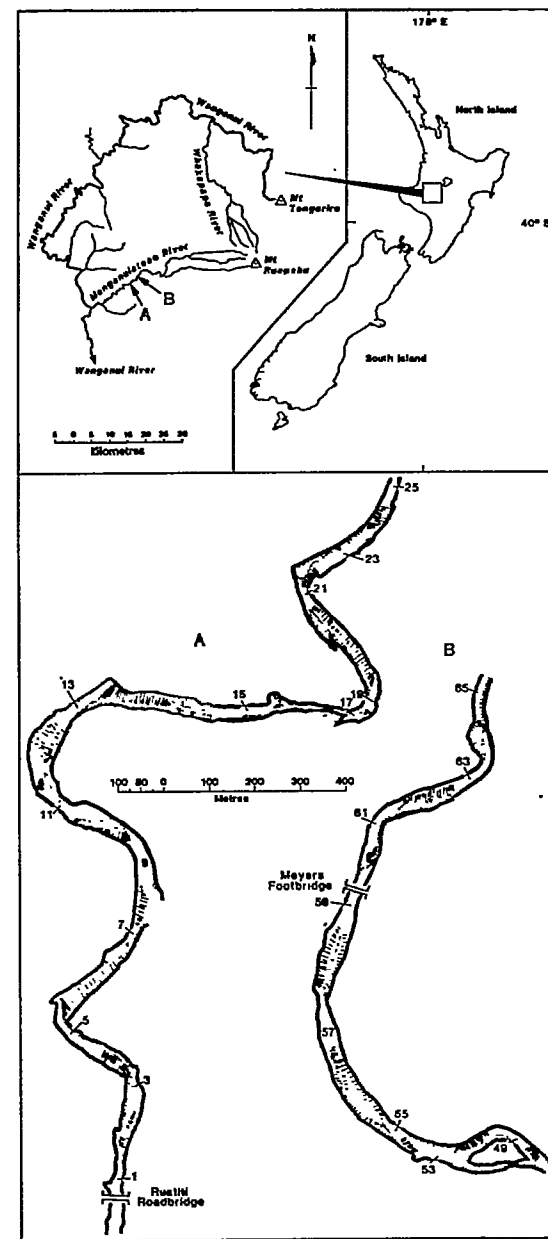


Fig. 4.1 Location of the Manganuiateao River study site within New Zealand. Throughout each day of each year of the study Blue Duck pairs occupied and defended territories that included several pools and rapids as indicated on two stretches of river (A and B). For example, two territories, occupied in all 14 years, encompassed pools 1 to 9, and 55 to 61. The smallest two territories included only pool 11, occupied for 15 months, and pools 49 to 55 for 3 years.

by one male and one female. Floater males were vigorously challenged and evicted by all territory-holding males.

Most Blue Ducks had only one mate (59% of 54 individuals) while others had up to four mates in a lifetime (mean 1.6, SD 0.8). Partnerships persisted from 6 months to 8 years but most included 1 or 2 years (mean 1.8 years, SD 1.7). Pair duration did not vary between first, second, or third pairings (*t*-tests 1.0–1.5, NS). Mate fidelity, as determined by pair members that survived from one breeding season to the next, was 88.7% (in 71 pair-years) and the probability of divorce was 11.3%.

Mechanism of pair formation

Three pair formation strategies were observed. Partnerships were initiated by the disruption of existing pair bonds forcing a divorce ($n = 13$), or the establishment of new territories by single individuals that attracted mates ($n = 12$ males, 4 females). Other pairs were formed when a dominant pair formed within a small aggregation of juveniles at an unoccupied location on the river ($n = 6$). Only males successfully disrupted pair bonds.

Territorial males, whose mate had recently died, usually adopted the most active strategy, forcing divorce in a neighbouring territory. These encounters involved aerial chases and prolonged and damaging fighting during which the female rarely intervened (Kear and Steel 1971; Eldridge 1985, 1986a).

Causes of mate change and divorce

The demise of 61% of pairings ($n = 36$) were due to the death or disappearance of one or both mates, while 39% were due to divorce.

Territorial males, whose mate had recently died, were responsible for 11 forced divorces by simply ousting the neighbouring male and occupying with his new mate most of her previous range and some of his former. New pairs appeared more vulnerable to these challenges; 5 of 7 pairs that persisted for less than 9 months and not over the breeding season, and 5 of 14 that had been together over only one breeding season were split in this way whereas only 3 of 15 more enduring pairings were disrupted (χ^2 contingency = 2.89, $0.1 > P > 0.05$).

The new partners of 14 females were generally older than their previous partner ($n = 7$) or were previous partners ($n = 3$) whose return challenges were successful (in one case 6 months and a breeding season later). In 12 cases the new mate had been resident in the adjacent territory and all but one had a previous breeding history.

There were two instances where female choice was apparent in the divorce event. One mate switch involved two yearlings who, for 4 months at the peak of the breeding season, occupied a vacant section of river at the lower extremity of the range occupied by Blue Ducks on the river and who made no detectable breeding attempt. While the male was

in wing moult, the female moved approximately 4 km upriver, 2 km above her natal range, to consort immediately with a territorial male whose mate had just died. Possibly in similar vein was the demise of a sibling pair which occupied a small range between two long-held territories for 15 months and over one breeding season in which they made no detectable breeding attempt. When the female on the adjacent territory died, her mate entered the young pair's range and was seen chasing the male and consorting with the female; she then moved to his territory. These are the only instances in which a female changed her range.

Correlates of reproductive success

Blue Duck breeding success varies annually depending on the severity of nest predation and winter/spring river flows (Williams 1991) and total reproductive failure across the population occurred in one of the 14 years of this study. In addition to year effects, we controlled for male age in the following analyses, as reproductive success increased throughout the age-classes for this sex (logistic regression $\Delta D = 5.93$, $\Delta df = 1$, $P < 0.02$). Young males produced fewer fledglings than middle-aged males which produced fewer than older males; for example, yearling males produced 0.5 fledglings per year (adjusted for year effects), 2–4-year-old males 1.1 fledglings, and 5+-year-old males 1.7 fledglings. Female reproductive success also increased with age; for example, yearling females produced 0.4 fledglings, 2–4-year-old females 1.3 fledglings, and 5+-year-old females 1.8 fledglings. Female age did not contribute significantly to variance in reproductive success of the pair when male age was included in the analyses ($\Delta D = 1.66$, $\Delta df = 1$, NS).

Familiarity with a partner

After controlling for year and age effects, the variation in reproductive success was not influenced by pair duration ($\chi^2 = 1.93$, $df = 1$, NS). However, the fitted values clearly increased between the first and eighth year pairs were together (Fig. 4.2), meeting the nonparametric criteria for a significant correlation (Spearman rank correlation, $r_s = 0.93$, $n = 8$, $P < 0.01$). Therefore, we suspect that pair familiarity in Blue Duck does influence a pair's reproductive potential.

Cost of mate change

In order to determine whether there was a cost to changing partners, the confounding effects of male age and year were removed in an analysis of fledging success in pairs with new or the same partners (i.e. the mate status). Reproductive success varied significantly with mate status ($\Delta D = 4.27$, $\Delta df = 1$, $P < 0.05$). For example, faithful mates produced a mean of 1.6 fledglings compared to a mean of 0.74 fledglings for new partnerships.

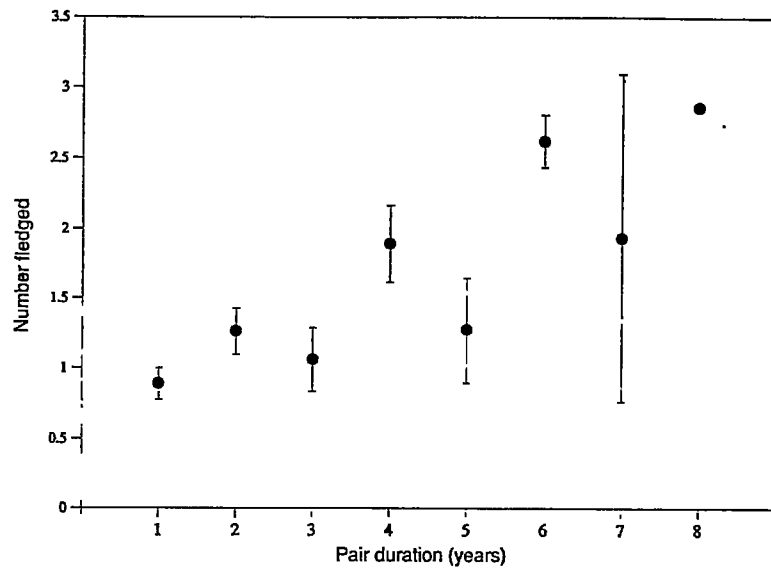


Fig. 4.2 Pair duration and reproductive success in Blue Ducks. The fitted values and standard errors are shown (Spearman rank correlation $r_s = 0.93$, $n = 8$ years, $P < 0.01$). Sample sizes for each point were 35, 20, 15, 9, 7, 5, 3, 1 pairs.

Correlates of divorce

There was little indication that prior reproductive histories influenced the probability of divorce in Blue Ducks. Considering pair members that survived over two consecutive breeding seasons, 11% of 28 divorced after reproductive failure and 14% of 37 separated after reproductive success. This difference was not significant.

Partner characteristics and reproduction

Yearling males tended to pair with females of the same age, but thereafter, and because of their longer lives, re-paired with younger females. Overall, in 19 (44%) of 43 different pairings males were older than females, in six (14%) females were older, in 11 (26%) partners were of similar ages (relative ages not known in seven (16%)). The most extreme example was a male at least 11 years old with a consort a mere 3 months on the wing!

The reproductive consequences of pairing with different aged partners is shown in Fig. 4.3. Any pair that contained a yearling of either sex reproduced poorly (mean 0.5 fledglings, SD 0.2) compared to when both partners were older (mean 1.7 fledglings, SD 0.5). In some pairings it was obvious that an older mate was advantageous. For both sexes the

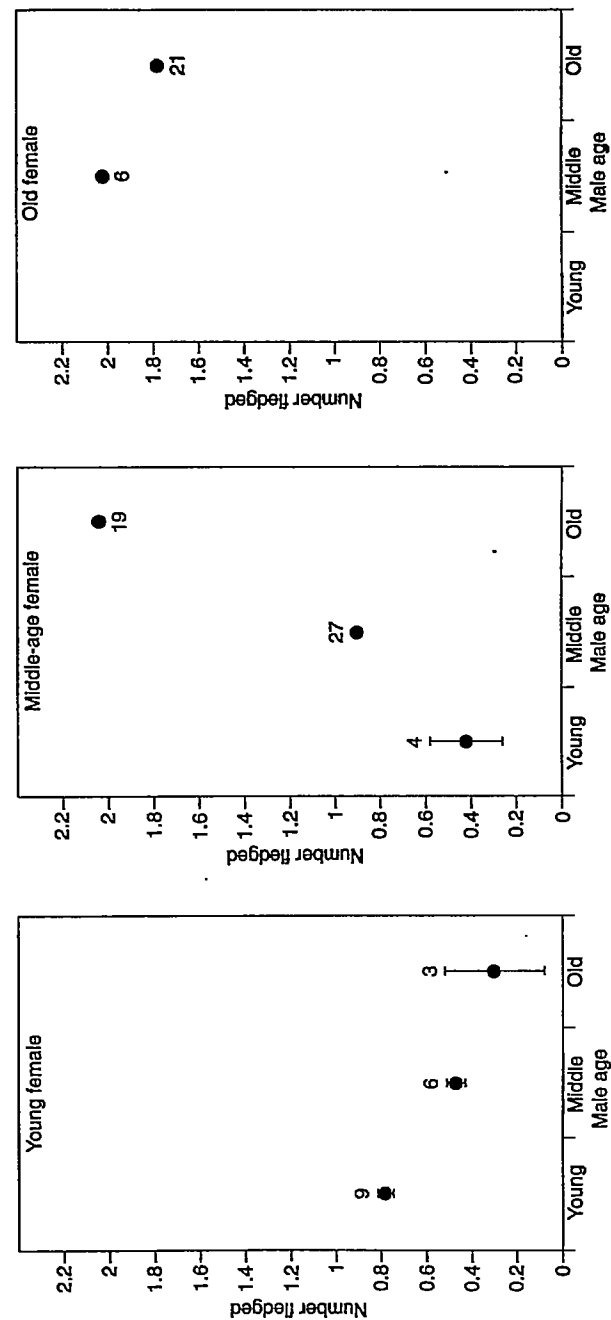


Fig. 4.3 The combined effect of male and female age on annual number of ducklings fledged, after controlling for year variation. Both male and female age effects were significant (logistic regression χ^2 males = 4.7, $df = 1$, $P < 0.05$; females = 5.6, $df = 1$, $P < 0.02$). Sample sizes accompany each point.

success of middle-aged birds increased with increasing mate age. The opposite trend was apparent for young birds; they performed less well with the older mates. Since male Blue Ducks live longer than females we would expect that they would achieve the preferred option (pairing with an older partner) more than would females.

Discussion

The riverine habitat

Blue Ducks occupy a distinctive habitat. Rivers, especially their fast-flowing sections, appear difficult for ducks to exploit; the vagaries of river flow may significantly affect food availability and be hazardous as breeding habitat by flooding nests and sweeping away young ducklings. Although many species of ducks make periodic use of rivers, only four species worldwide have adapted to year-round river life dependent solely on riverine resources.

In some sections of New Zealand rivers, the aquatic invertebrate fauna upon which Blue Ducks feed (Collier 1991) is diverse and abundant, occurring at densities which enable Blue Ducks year-round to obtain their energetic requirements from within a small area and with limited feeding effort (Veltman and Williams 1990; Veltman *et al.* 1991). Energetic costs and risks arising from moving between many widely spaced feeding sites can thus be avoided. Other resources essential for year-round habitation, for example, safe feeding areas for ducklings, protective riverbank vegetation, cavities or caves for nesting, resting, moulting, or hiding can be found within discrete sections of river. Middle and upper zones of New Zealand rivers include many sections with all the resources required. Year-round exploitation implies permanent residency, and sections of river, by having only two major points of intrusion by conspecifics—the upper and lower extremities of the territory—are economically defensible. The river's openness allows an occupant to be visible and to advertise its presence while making intruders easy to detect. Under these circumstances, a year-round territorial spacing system is favoured.

Territoriality and the mating system

Oring and Saylor (1992) stress the intimate connections between spatial organization, mating relationships, and the nature of parental care in shaping waterfowl social systems. In the case of the Blue Duck, we see three major effects of territoriality on the mating system. Exclusive ownership of resources would limit breeding opportunity to territory-holders. Co-operation between mates would be favoured to prevent territory take-over by other pairs, but not necessarily so in response to intrusions by single birds when territory eviction is not threatened. Prolonged investment in a single mate promotes co-operation in defence

and enhances both breeding opportunity and performance, especially important during egg formation and laying, and brood rearing.

Restriction of breeding opportunity

The subdivision of suitable riverine habitat into a series of exclusively occupied and defended segments restricts non-territorial individuals to an itinerant and furtive existence that denies breeding opportunity. Intense competition for that exclusive space, and obvious attempts at obtaining it as soon as possible, are indicated by the strong philopatry of both sexes (the area best known is the area of birth), instances of just-fledged juveniles consorting with and eventually pairing with solitary territory-holders, and examples (given above) of young pairs holding territories before being physiologically capable of breeding. The importance of having a partner with whom to co-operate in defence of the territory against intruding pairs and ensure certainty of breeding opportunity is emphasized by territorial males, upon the death of their mate, immediately attempting to steal a neighbour's irrespective of time of year (including one case while the female was incubating, another during care of a young brood, and two immediately prior to laying), and their ready acceptance of newly fledged juveniles as potential partners. Temporary liaisons with neighbours when existing partners are vulnerable to eviction (e.g. during wing moult) may also serve this purpose (Eldridge 1986a).

Costs and benefits of divorce

If an individual's only chance to breed is as a member of a territory-holding pair, then those with the opportunity should vigorously defend their territory. Co-operation between partners in challenging intruders is obviously advantageous when challenges come from a pair. However, although partners should stay alert to opportunities to switch mates when the pair bond is threatened by a single intruder (which may explain why in many instances they do not show strong aggressiveness to intruders of the opposite sex), there are obvious reproductive costs in doing so. For example, we have identified that the initial breeding effort with a new partner is less productive than a further attempt with the existing mate, and pair familiarity increases reproductive success. Significantly, there was a tendency for new pairings and those comprising young birds to be more readily disrupted than longer-established ones comprising older birds.

For young females, however, the reproductive costs of divorce may be minor. A partnership with an older, established territory-holder (and possibly proven breeder) is likely to be more enduring, and thus more productive, than one with a young male. The relative shortage of females within the study population provides most females with the opportunity to pair with older males. Old females, on the other hand, have much to

lose from a change of mate and are predicted to be more co-operative in territorial defence. Enduring pair bonds and enduring residency on a particular territory separately and/or together may enhance reproductive success through familiarity with territorial resources. For example, the feeding locations and ranges of experienced parents with their broods are more consistent day by day than those of new parents or new territory occupants (M. Williams, unpublished data). A more precise knowledge of a territory's resources may be especially important during prolonged river spate when food is scarce.

Prolonged breeding effort

The breeding effort demands a long annual contribution from both sexes. In contrast to most other ducks, but in common with other river specialists, the reproductive effort of Blue Ducks extends over about 45% of the year (Williams 1991). Prior to and during egg laying, the pair reduce their range within the territory and the male is especially belligerent towards intruders of either sex and ducks of other species as he guards his mate and his breeding opportunity. Further support of the reproductive effort is demanded by the ever-present hazard of the river current to duckling survival; separated ducklings rarely survive, and if they do, fledge considerably lighter than those raised with biparental care (Williams 1991). In response to this hazard, selection has favoured a significant male contribution to care of the brood (Veltman and Williams 1990).

Comparisons with other riverine waterfowl

Three other ducks, the Torrent Duck *Merganetta armata*, African Black Duck *Anas sparsa*, and Salvadori's Duck *Salvadorina waigiensis*, are also river specialists. Torrent Ducks share similar spatial and mating systems, evidence of a common response to common ecological influences. For example, Torrent Ducks are dispersed as pairs on discrete territories (Johnsgard 1966) and although both birds co-operate in territorial defence, Eldridge (1986b) noted the tendency for the individual partners to react more strongly to intruders of the same sex. Males contribute fully to brood care (Moffett 1970). Salvadori's Duck from the highlands of New Guinea has been little studied but is dispersed as discrete territorial pairs along the rivers, males contribute to care of the young, and pairs occupy and defend territories year-round (Kear 1975). African Black Ducks, as pairs, defend discrete, nonoverlapping territories year-round (Ball *et al.* 1978; McKinney *et al.* 1978). Pair bonds, some of which persist over several years, are frequently tested and disrupted (Ball *et al.* 1978). At times, pair bonds appear to weaken (e.g. during moult or when the partner is injured) and individuals may form temporary liaisons with neighbours or other birds. Such liaisons may provide opportunities to assess alternative mates or they may be useful in preventing eviction

from a territory. Breeding is restricted to territory-holders. In contrast to other river specialists, male African Black Ducks do not contribute parental care to the brood although they remain in contact with the female throughout (McKinney *et al.* 1978). The riverine habitat of this species is considerably more tranquil than that of the other three river ducks thus posing less of a hazard to brood survival and the basic *Anas* pattern of female-only brood care persists. This suggests male parental care is a by-product of year-round territoriality and mate fidelity and occurs only in those species inhabiting environments hazardous to ducklings where male participation confers a clear selective advantage (McKinney 1991).

Why strict monogamy?

Forced extra-pair copulations (FEPCs) occur in many duck species and mixed male reproductive strategies (monogamy + FEPC) appear to be common in Anatidae (McKinney *et al.* 1983; Afton 1985; Everts and Williams 1987; Sorenson 1994). There are no observations of FEPC attempts in African Black Ducks (McKinney *et al.* 1978) or Blue Ducks (Williams 1991), and no evidence of extra-pair fertilizations in Blue Ducks (Triggs *et al.* 1991). We believe that FEPC is incompatible with the social system of river specialists. Paired territory-holding males give priority to guarding mate plus territory, especially during the breeding season, and the extra-pair excursions that would be needed to monitor the breeding status of females on neighbouring territories and to attempt FEPCs on fertile females apparently entail costs and risks that males cannot afford.

Long-term pair bonds in other ducks

Monogamy, involving seasonal or long-term pair bonds, is the primary mating system in most waterfowl (Oring and Saylor 1992). Seasonal pair bonds are characteristic of migratory Holarctic ducks (*Anas*, *Aythya*, *Mergus*, *Aix*) in which males desert their mates during the breeding season, leaving the females to care for the ducklings alone, and new bonds form while the birds are in flocks on the wintering areas. As well as being usual in geese and swans, long-term pair bonds are believed to be characteristic of whistling ducks (*Dendrocygnini*), shelducks and sheldgeese (*Tadornini*), and certain tropical and Southern Hemisphere ducks, although this belief is based on data from wild populations of only a few species (Table 4.1). Long-term partnerships are suspected to occur also in steamer ducks (*Tachyerini*), Torrent Ducks and in certain southern ducks with biparental care (Brazilian Merganser *Mergus octosetaceus*, Silver Teal *Anas versicolor*, Chiloe Wigeon *A. sibilatrix*, Bronze-winged Duck *A. specularis*, Chestnut Teal *A. castanea*, Brown Teal *A. chlorotis*, Crested Duck *Lophonetta specularioides*, Salvadori's Duck). In most ducks, pair formation occurs away from the breeding

Table 4.1 Statistics for long-term pair bonds and probability of divorce in 19 ducks and sheldgeese

| Species | No. pairs | Pair-years | Number of divorce events | Probability of divorce | Biparental care? | Source |
|--|-----------|------------|--------------------------|------------------------|------------------|--------|
| Continuous partnerships | | | | | | |
| Black-bellied Whistling Duck | 19 | 19 | 2 | 10.5 | Yes | 1 |
| <i>Dendrocygna autumnalis</i> | 106 | 123+ | 2 | — | | 2 |
| Magellan Goose | | | | | | |
| <i>Chloephaga picta</i> | 13 | 13 | 2 | 15.4 | Yes | 3 |
| Mand Duck | | | | | | |
| <i>Chenonetta jubata</i> | 6 | 6 | 0 | 0 | Yes | 4 |
| African Black Duck | | | | | | |
| <i>Anas sparsa</i> | 7 | 10 | 1 | 10.0 | No | 5 |
| Blue Duck (sedentary) | | | | | | |
| <i>Hymenolaimus malacorhynchos</i> | 28 | 71 | 8 | 11.3 | Yes | 6 |
| Part-time partnerships; mates reunite on breeding area | | | | | | |
| Shelduck | 71 | 130 | — | — | Yes | 7 |
| <i>Tadorna tadorna</i> | 41 | 41 | 8 | 19.5 | | 8 |
| Australian Shelduck | | | | | | |
| <i>Tadorna tadornoides</i> | 21 | 63+ | — | — | Yes | 9 |
| White-checked Pintail (sedentary) | | | | | | |
| <i>Anas bahamensis</i> | 36 | 44 | 15 | 34.1 | No | 10/11 |
| Laysan Duck (sedentary) | | | | | | |
| <i>Anas laysanensis</i> | 11 | 11 | 3 | 27.3 | No | 12 |
| Mallard (urban, sedentary) | | | | | | |
| <i>Anas platyrhynchos</i> | 8 | 11 | 1 | 9.1 | No | 13 |
| Part-time partnerships; mates reunite on wintering area | | | | | | |
| Bufflehead | | | | | | |
| <i>Bucephala albeola</i> | 2 | 5 | — | — | No | 14 |
| Barrow's Goldeneye | | | | | | |
| <i>Bucephala islandica</i> | 6 | 6 | 1 | 16.7 | No | 15 |
| European Wigeon | | | | | | |
| <i>Anas penelope</i> | 3 | 4 | — | — | No | 16 |
| Long-term bonds frequent; mechanism unknown | | | | | | |
| Speckled Teal | | | | | | |
| <i>Anas flavirostris</i> | 28 | 47 | 4 | 8.5 | Yes | 17 |
| Cape Teal | | | | | | |
| <i>Anas capensis</i> | 4 | 14 | — | — | Yes | 18 |
| Grey Teal | | | | | | |
| <i>Anas gibberifrons gracilis</i> | 7 | 17 | — | — | Yes | 19 |

Note: the terms pair-years and probability of divorce are defined in Chapter 1.

Sources: 1. Bolen (1971); 2. Delnicki (1983); 3. Summers (1983); 4. Kingsford (1990); 5. Ball *et al.* (1978); 6. this study; 7. Young (1864); 8. Williams (1973); 9. Riggert (1977); 10. Sorenson (1992); 11. Sorenson *et al.* (unpublished); 12. Moulton and Weller (1984); 13. Mjelstad and Sattersdal (1990); 14. Gauthier (1987); 15. Savard (1985); 16. C. R. Mitchell (unpublished); 17. J. Port (unpublished); 18. Siegfried *et al.* (1976); 19. Marchant and Higgins (1990).

grounds, females are strongly philopatric, and each male follows his mate back to her familiar nesting area (Rohwer and Anderson 1988; Anderson *et al.* 1992; McKinney 1992). In species where males desert their mates, pair bonds apparently can persist only if breeding partners are able to rendezvous and reunite at some point before the next breeding season, for example at the breeding area before birds leave, at wintering or migratory stop-over sites, or at the breeding area after birds return. Reuniting of mates on the wintering grounds has been recorded in two migratory species of sea ducks (Mergini: genus *Bucephala*; Savard 1985; Gauthier 1987) and this pattern may be more widespread in this tribe. C. R. Mitchell (in litt.) recorded a few cases of European Wigeon *Anas penelope* pair members reuniting in a subsequent year at super-rich wintering sites, where supplemental feeds were provided. Although mate fidelity has been recorded in some other migratory *Anas* species (Dwyer *et al.* 1973; Fedynich and Godfrey 1989; Seymour 1991), it appears to be rare because pair formation takes place in large flocks (where mates may not encounter each other) and competition between males for mates is strong because of male-biased sex ratios. Mate fidelity can be more frequent in sedentary *Anas* populations (Moulton and Weller 1984; Sorenson 1992; Mjelstad and Saetersdal 1990) (Table 4.1). Reuniting of mates after return to the breeding area occurs in three shelduck species (Tadornini: genus *Tadorna*; Young 1964; Williams 1973, 1979; Riggert 1977) and this pattern may be more widespread in this tribe. Banding studies on breeding adults of seven migratory North American *Anas* and *Aythya* species showed that males returned to the same areas at lower rates (1.0–10.5%) than females (14.7–74.5%), and nearly all returning males were unpaired (Anderson *et al.* 1992).

Persistent pair bonds occur regularly in certain *Anas* species living in tropical and Southern Hemisphere regions where breeding seasons are often extended and/or irregular and many populations are nonmigratory (McKinney 1991; Sorenson 1991). Three studies of *Anas* species with strongly developed biparental brood care (*capensis*, *gibberifrons gracilis*, *flavirostris*) indicated a high incidence of long-term partnerships (Siegfried *et al.* 1976; Marchant and Higgins 1990; J. Port unpublished data), while data for two sedentary species with female-only brood care (*laysanensis*, *bahamensis*) showed a much higher proportion of pairs that divorce (Moulton and Weller 1984; Sorenson 1992).

In Table 4.1, biparental care is recorded in four of five species with continuous partnerships, all three species with long-term but uncertain pair bonds, but only two of eight species in which bonds break annually. Of these species, Tadornini (2), Dendrocygnini (1) and Cairinini (1) exhibit biparental care, one of the Mergini species does not, and only about half of the *Anas* species do so. The probability of divorce ranged between 0% and 34.1%, mean of 14.0% (SE 2.7). Species with biparental care were generally less likely to divorce (mean 9.4%) than

those with female-only care (mean 19.4%). Thus, there are preliminary indications that mate fidelity and phylogeny may be associated to some degree with patterns of parental care. Analyses of the relative importance of these factors will not be possible without evidence for many more species.

Sorenson's (1992) study has addressed the possibility of a relationship between divorce and breeding success but no such relationship was found. Probability of divorce rates were similar among pairs of White-cheeked Pintails *Anas bahamensis* that were successful in raising ducklings (7 of 11 pairs) and those that were unsuccessful (6 of 12 pairs).

The early stages of pair formation in young, inexperienced ducks (less than 1 year old in *Anas* and *Aythya*, less than 2 years old in Tadornini) involve temporary bonds as described for Barnacle Geese *Branta leucopsis* (Choudhury and Black 1993), and divorce is preceded by extra-pair courtship and liaisons with the new mate (McKinney 1992). Many duck populations have male-biased adult sex ratios and males tend to be the most active sex in courtship. Chiloe Wigeon *Anas sibilatrix* are an extreme example: unpaired males begin to court females while they are still ducklings, apparently because adult females which are already paired are no longer available (Brewer 1991). The usurping of mates by male take-over, as described for Blue Duck and African Black Duck, is an unlikely strategy for nonterritorial ducks and has not been described. Several shelduck species are unusual in having female-biased sex ratios and females compete actively with one another for mates.

The comparative evidence for long-term pair bonds in ducks is still scarce and studies of Southern Hemisphere species are especially needed. The strong linkage that has been assumed between the incidence of long-term pair bonds (see Chapter 3) and the incidence of biparental care should be examined carefully, and attention should be given to the behavioural mechanisms involved in mate acquisition and mate fidelity.

Summary

Most Blue Ducks had one mate in a lifetime, usually lasting for 2, but sometimes up to 8, years. Reproductive success of pairs tended to increase with pair duration after controlling for year and age effects. A common cause of mate change (39%) was usurpation by neighbouring males that had lost their mates. These lone males were usually older than victim males. In addition to losing their mates, victim males lost their territory to the usurper. Divorce was not related to the pairs' prior reproductive failure/success. Ducks that changed mates had fewer fledglings the next year. Pairs with one young member bred less well than pairs with two experienced mates. Considering data from 11 duck and shelduck species the probability of divorce ranged between 0% and

34.1%, mean of 14.0%. Species with biparental care were apparently less likely to divorce (probability of 9.4%) than those with female-only care (probability of 19.4%).

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