Territorial behaviour, forced copulations and mixed reproductive strategy in ducks

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Introduction

The concept of mixed reproductive strategy has received considerable attention since it was first proposed by Trivers (1972), e.g. Beecher and Beecher (1979), KcKinney *et al.* (1983), Fitch and Shugart (1984). In birds, there is growing evidence that extra-pair copulations are part of a mixed reproductive strategy of paired males (Beecher and Beecher 1979; McKinney *et al.* 1984; Afton 1985; Westneat 1987). Extra-pair copulations have been reported in many species but it is in the Anatidae (ducks and geese) that they are common (McKinney *et al.* 1983). In ducks, extra-pair copulations are commonly referred as forced copulations because successful mounting by males may occur even if females are unwilling to cooperate. Recent evidence indicates that forced copulations can result in successful fertilisations (Burns *et al.* 1980; Evarts and Williams 1987).

The counter-strategy to extra-pair copulations adopted by paired males is mate guarding in many non-anatids (Beecher and Beecher 1979; Birkhead 1979; Carlson *et al.* 1985; Hatch 1987; Moller 1987) and in ducks (Goodburn 1984). As we would expect, mate guarding is well developed in ducks as many species exhibit a mate defence territoriality (McKinney 1986). However, there is considerable variability in the intensity of mate guarding and territoriality, and much of this variance remains unexplained. Forced copulations appear to be absent in some highly territorial species of ducks (McKinney *et al.* 1983; McKinney 1985; Gauthier 1986).

In this paper, the variability in territoriality and in the occurrence of forced copulations in ducks (sub-family Anatinae) are reviewed. An attempt is then made to explain this variability by proposing a model of mixed reproductive strategy in males based on environmental variance.

Territorial behaviour and mate guarding in ducks

The sub-family Anatinae includes 103 species separated in 8 tribes (Johnsgard 1978).

Sheldgeese (genus *Cyanochen*, *Neochen*, *Chloephaga*, and *Alopochen*) have been excluded from this review because they are ecological equivalents of true geese. Ducks predominantly inhabit temperate and sub-arctic wetlands, and most species are migratory. In the northern hemisphere, ducks generally pair on the wintering grounds, well before the start of the breeding season. Unlike most other bird species, the female is the sex attached to the birth place (philopatric), and the male follows the female when she returns there during the spring migration. Once on the breeding grounds, only paired males are territorial. Lone males, however, are always present on the breeding ground but they never defend territories. A territory of a particular quality is thus not a pre-requisite for the acquisition of a mate. Pair bonds usually break after females have completed egg-laying, although the exact timing of the rupture varies among species. Males then leave for moulting grounds while females incubate the clutch and raise the young alone. In several southern hemisphere species, however, pair bonds often last well into the brooding period or may persist for more than one breeding season, and parental care may be shared by both parents. Although some species also defend brood territories (Ball *et al.* 1978; Savard 1982; Gauthier 1987a), the present paper is limited to the territory defended by paired males from the pre-laying to the incubation stage.

The occurrence of territoriality in ducks has long been debated (Hochbaum 1944; Dzubin 1955; Sowls 1955). In dabbling ducks, Titman and Seymour (1981) showed the existence of a gradient of territoriality from a weak mate defence in species like the Northern Pintail *Anas acuta* to strong territorial behaviour in the Northern Shoveler *A. Clypeata*. However, there is no sharp distinction between mate defence and territory defence in ducks (see below), and both may be considered as different degree of territoriality.

Four degrees of territoriality can be recognised (Figure 1). Type 1 species show little territorial behaviour during the breeding season. Males are not very aggres-
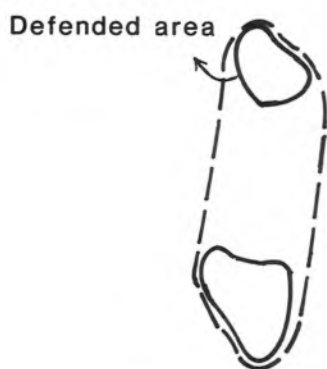
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Home range
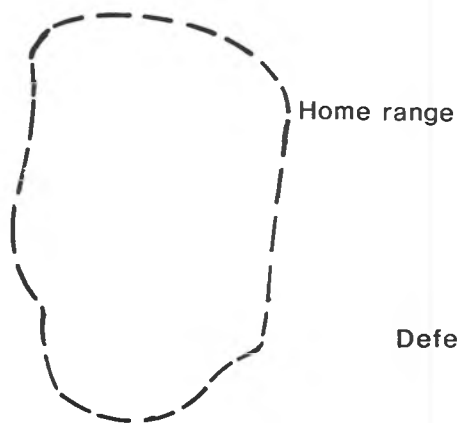
Defended area

Type 1

No defended area
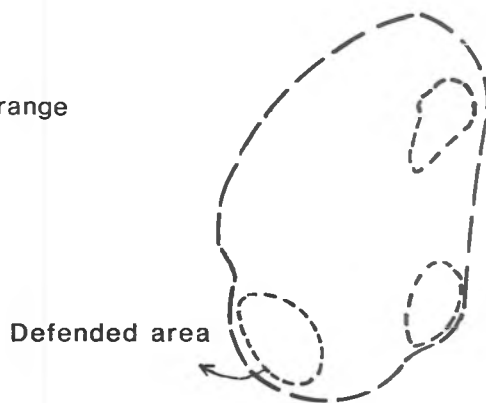
Type 2

Loosely defended
"moving territory"

Defended area

Type 3

Strongly defended
"moving territory"

Type 4

Highly site-specific
territory

Figure 1. Illustration of the types of territories defended in ducks (see text for details).

sive, home ranges of pairs are large and overlapping with no exclusive areas, and there are few signs of a defended area. The Northern Pintail (McKinney 1973; Derrickson 1978) and Green-winged Teal *A. crecca* (McKinney and Stolen 1982) exemplify this system.

Males of type 2 species are moderately aggressive and defend a moving territory around the female within their home range. This is found in species like Mallard *A. platyrhynchos* (Titman 1983) and Gadwall *A. strepera* (Dwyer 1974). The expression "moving territory" was first applied to ducks by Dzubin (1955). Although the term has been criticised, it nonetheless describes this behaviour well; in these species, there is clearly a defended area, but this area shifts through time and is often not exclusive (Titman 1983).

Type 3 species also defend a moving territory around the female. However, males are much more aggressive, the defended area is more site-specific, more exclusive, and sometimes has well-defined boundaries. Pairs nonetheless spend some time feeding outside the territory. This system is found in American Black Duck *A. rubripes* (Seymour and Titman 1978), Blue-winged Teal *A. discors* (Stewart and Titman 1980) and Northern Shoveler (Poston 1974; Seymour 1974a, b).

Finally, type 4 species have a very strong territorial system. Males are extremely aggressive and defend a small, well-defined area where all conspecifics but the mate are excluded. All activities of the pair are restricted to the territory. The African Black Duck *A. sparsa* (Ball *et al.* 1978), Bufflehead *Bucephala albeola* (Donaghey 1975; Gauthier 1987c), Common and Barrow's Goldeneyes *B. clangula* and *B. islandica* (Savard 1982, 1984) and Common Shelduck *Tadorna tadora* (Young 1970; Patterson 1982) exhibit this type of territoriality.

Although this classification illustrates the variability in territorial behaviour among ducks well, it is important to point out that all species do not clearly fall into any one type. In reality, there is a gradient from non-territorial species to highly territorial ones. Furthermore, one species may exhibit varying degrees of territoriality in different habitats (Dzubin 1955; Nudds and Ankney 1982).

In ducks, protection of the female from harassment by conspecific males and vigi-lance for predators are important roles of paired males (Ashcroft 1976; Patterson 1982; McKinney 1985; Gauthier 1987c). Exclusive defence of a female is especially advantageous to males because the adult sex ratio is strongly male-biased in most species of ducks (Bellrose *et al.* 1961; Aldrich 1973). In weakly or moderately territorial species (types 1 to 3), the territory is clearly focused on the female, and the male essentially defends an area around the female. In highly territorial species (type 4 and some type 3), defence of an area around the female has evolved into the defence of an area *per se*. Although the territory is defended by the male even in the absence of the female (e.g. when she is on the nest), the territory is quickly abandoned by the male if the female is removed permanently. This suggests that, even in highly territorial species, the female is the principal resource defended by territorial males.

Defence of a territory in ducks provides the following benefits: i) through male vigilance it protects the female from harassment by conspecifics and from predators thus increasing the chance that she will nest successfully, ii) provides her with an undisturbed feeding area and, iii) ensures the male's paternity through mate guarding (Gauthier 1987c). Although defence of food resources or of the nest site are benefits that can be important in some species (e.g. McKinney *et al.* 1978; Gauthier 1987c), current evidence suggests that territorial behaviour in ducks is essentially a female-defence system.

Mating strategies in ducks

The most prevalent mating system in ducks is seasonal monogamy (McKinney *et al.* 1983; McKinney 1986). In most migratory species, new pair bonds are formed every winter, although recent evidence suggests that long-term pair bonds may be more common that previously thought (e.g. Dwyer *et al.* 1973; Savard 1985; Gauthier 1987b). Although males associate closely with their mate throughout the duration of the pair bond (e.g. Anderson 1984), two other mating tactics are available to males: polygyny and forced copulations.

Polygyny is rare in wild populations of waterfowl (McKinney *et al.* 1983). A male-biased sex ratio and fairly synchronous breeding are two factors that are likely to

reduce the availability of fertilisable females (McKinney 1985; Gauthier 1986), and thus decrease the potential for polygyny (Emlen and Oring 1977) in ducks. Recent evidence nonetheless suggests that polygyny may be a secondary mating tactic pursued by initially monogamous males (Ohde *et al.* 1983; Anderson 1985; Gauthier 1986; Savard 1986).

Forced copulations are common in ducks (McKinney *et al.* 1983) and several lines of evidence suggest that they are a secondary mating tactic. First, forced copulations are performed mostly by paired males; the main goal of unpaired males is to court females and pair with them (McKinney *et al.* 1983; Afton 1985). Second, forced copulation attempts are directed mostly to prelaying and laying females i.e. fertilisable females (Cheng *et al.* 1982; Afton 1985). Third, paired males often defend their mate during forced copulation attempts (McKinney *et al.* 1983). Finally, inseminations resulting from forced copulation can fertilise eggs even if the action is performed without the cooperation of the female (Burns *et al.* 1980; Evarts and Williams 1987).

This evidence suggests that forced copulations are part of the mixed reproductive strategy of monogamous males. Field observations in species like Mallard, Northern Pintail and Lesser Scaup *Aythya affinis* strongly support this hypothesis (McKinney *et al.* 1983; Afton 1985). However, the frequency of forced copulation attempts varies widely among different species. In fact, there appears to be an inverse relationship between the degree of territoriality and the frequency of forced copulation (McKinney *et al.* 1983). Forced copulation attempts are common in weakly territorial species (types 1 and 2), but are rare in more territorial species (types 3 and 4). In fact, despite intensive field observations, forced copulation attempts were never observed in strongly territorial species (type 4) like the African Black Duck (McKinney *et al.* 1978), Barrow's Goldeneye (Savard 1985) and Bufflehead (Gauthier 1986).

Habitat variability and reproductive strategy

Ducks inhabit a great diversity of habitats such as shallow ponds, lakes, rivers, estuaries, marshes, mangroves and open sea. Some species like the Torrent Duck *Merganetta armata*, Salvadori's Duck *Anas waigiuensis* and African Black Duck are habitat specialists and are restricted to fast-flowing rivers (Kear 1975; McKinney *et al* 1978; Eldridge 1986a). At the other end of the scale, species like the Mallard and Grey Teal *A. gibberifrons* are generalists that breed in a wide variety of habitats subject to unpredictable fluctuations in rainfall and wetland conditions (Frith 1967; Bellrose 1979).

Habitat variability can have a profound influence on reproductive success. This is well documented in prairie-nesting ducks of North America. In most of these species, temporary and semi-permanent wetlands are the preferred habitat (Stewart and Kantrud 1973; Gilmer *et al* 1975), and nesting effort and reproductive success are strongly correlated with local wetland conditions in spring. In years of drought, a high proportion of females do not attempt to breed, desertion rates increase, and predators often gain access to normally secure nesting

Table 1. **Association between habitat variability and the type of territory defended by the male during the breeding season in 64 species of ducks.**

Habitat	Type of territory*			
	Type 1	Type 2	Type 3	Type 4
Stable	6	11	11	21
Variable	5	8	2	0

$$X^2_{adj} = 10.46,\ P<0.01,\ df = 1$$

* See Figure 1 for types of territories.
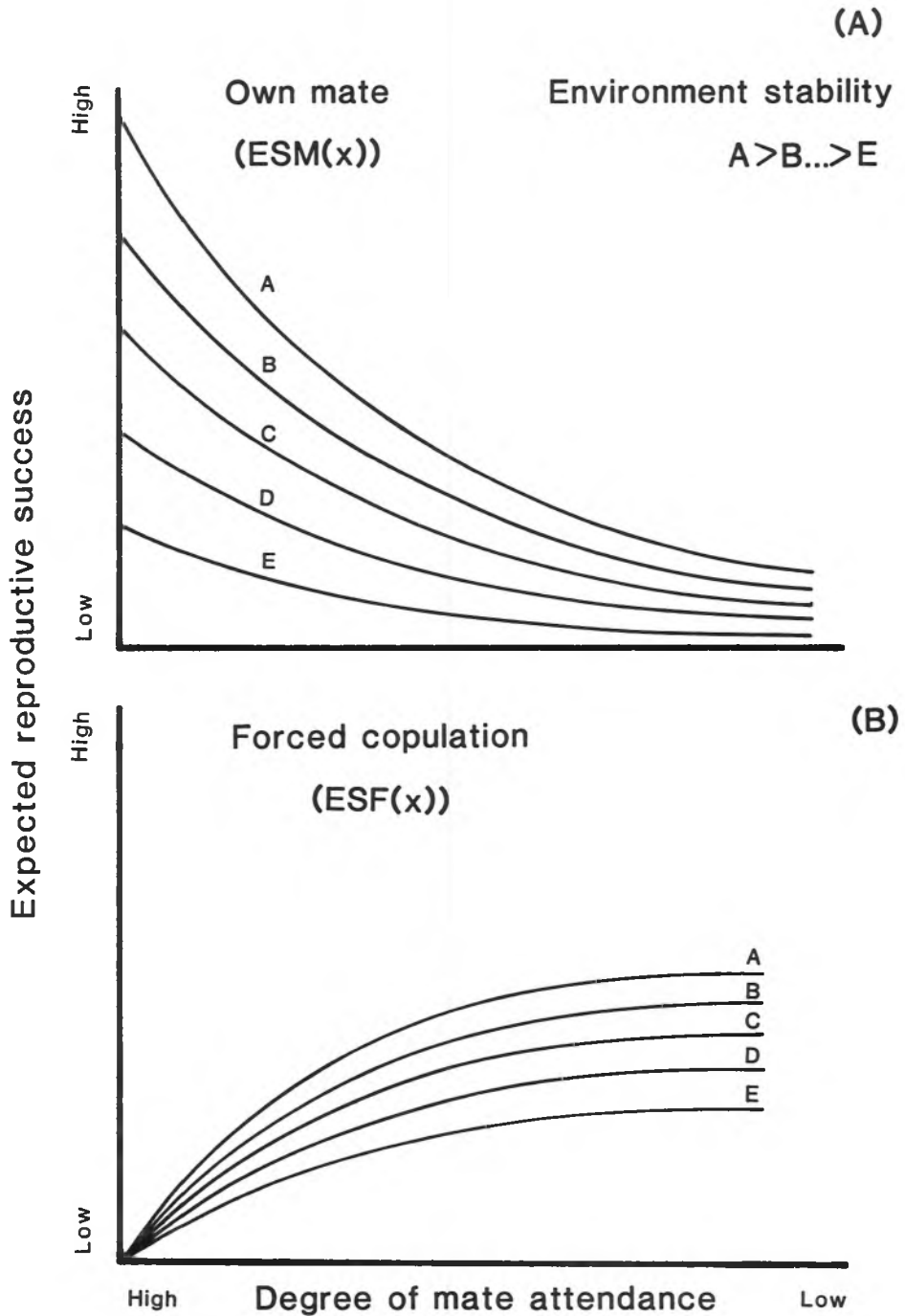 Numbers are those of species.

Figure 2 (i)   A graphical model to explain the evolution of territorial behaviour in ducks. (A) Expected reproductive success of paired males with their mate, (B) expected reproductive success of paired males through forced copulations.
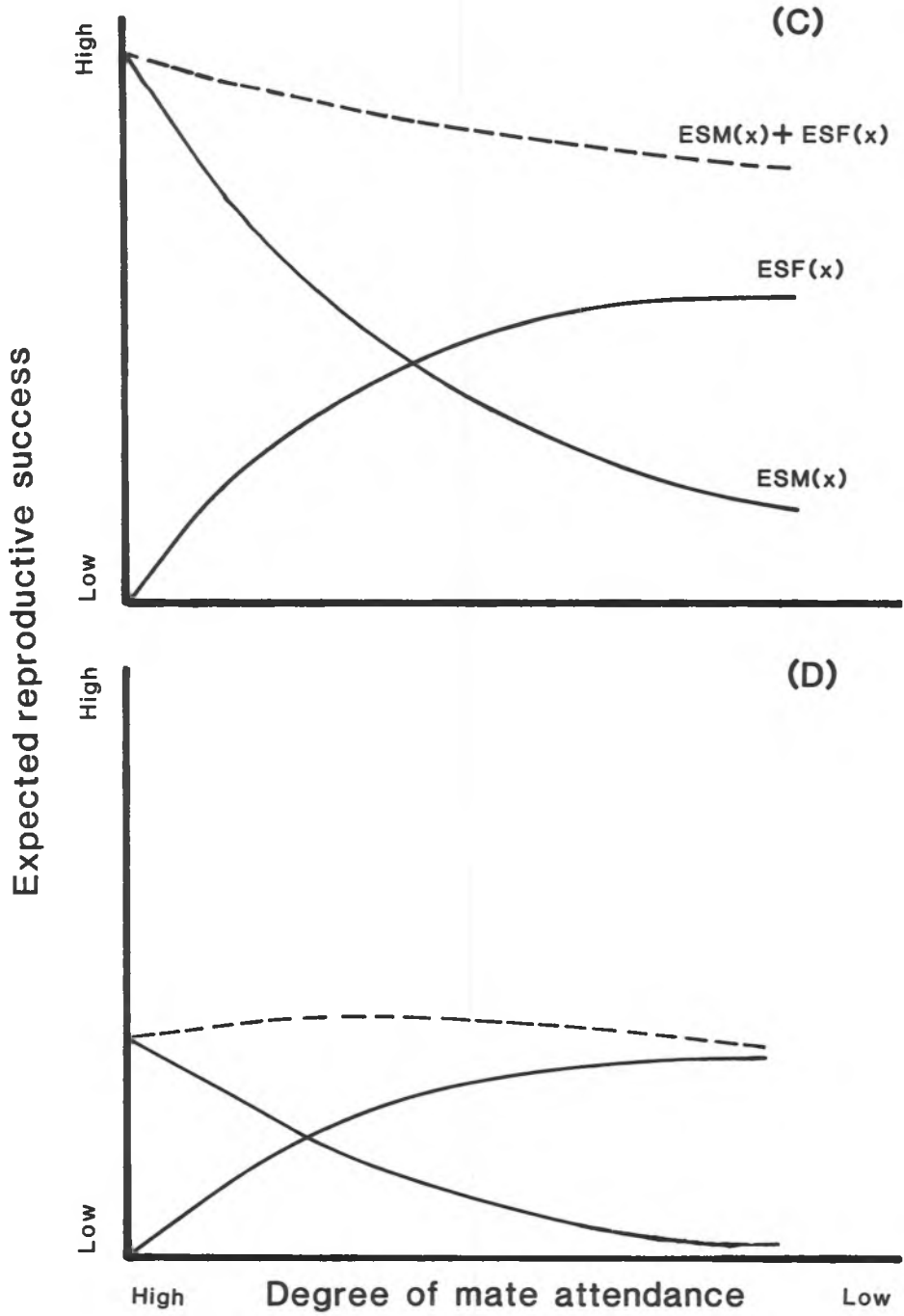
Figure 2 (ii) A graphical model to explain the evolution of territorial behaviour in ducks. (C) total expected reproductive success of paired males in a stable habitat, (D) total expected reproductive success of paired males in a variable habitat.

sites, such as islands in dried-out ponds, (Krapu *et al.* 1983; Cowardin *et al.* 1985). Therefore, reproductive success should, on average, be lower, and especially more variable in unpredictable habitats such as the temporary wetlands of the prairies.

McKinney (1965) was the first to relate the territorial system of ducks to variability in their habitat. He noted that Northern Shovelers are territorial and they use mostly permanent ponds, whereas Northern Pintails are not territorial and they prefer temporary ponds (McKinney 1973, 1975). An attempt was made to test McKinney's idea by extending the classification of territorial systems (Figure 1) to all species of ducks. Type of territorial behaviour exhibited by 64 of the 103 species of Anatinae could be classified (see Appendix). The preferred breeding habitat of each species was broadly classified as being stable (estuaries, coast, rivers, streams, and permanent marshes, ponds and lakes) or variable (floodplain and seasonal ponds and lakes). Variable habitats are defined as ephemeral wetlands which dry out more or less rapidly in the course of the breeding season depending upon weather conditions.

A significant association was found between the type of territory defended and habitat variability (Table 1). All but two strongly territorial (types 3 and 4) species occur in stable habitats such as deep lakes and estuaries (e.g. *Tadorna* sp.), coastal regions (e.g. *Tachyeres* sp.), mountain rivers (e.g. *Anas sparsa*), and permanent ponds (e.g. *Bucephala* sp.). Although only two species occurring in variable habitats appear territorial, many species using stable habitats are only weakly territorial (types 1 or 2). For instance, territories are conspicuously absent from the tribe Aythyini.

Such a test is obviously preliminary as this review is subject to many biases. For instance, territoriality is uncertain in several species and not studied at all in others. Further, territorial species may be over-represented in this sample, because territorial displays are usually conspicuous and thus more likely to be reported in the literature. However, there is clear support for McKinney's contention that territoriality is primarily associated with stable habitats in ducks.

Based on Brown's (1964) model, McKinney further hypothesised that the degree of territoriality in ducks is a function of the defendability of the food resources (see also Nudds and Ankney 1982). In a stable environment, a predictable food supply would be economically defendable and would account for territoriality. An alternative hypothesis can be suggested which explains the diversity of territorial behaviour in ducks. This hypothesis rests on the assumptions that forced copulation is a secondary mating tactic of paired males and that territoriality is primarily a female-defence system (see above).

A model of mixed reproductive strategy in ducks

It is hypothesised that variability in the nesting success of females, and therefore in the expected fitness gain of paired males, determines whether males will be territorial or not. This model can be shown graphically (Figure 2). ESM(x) is defined as the average expected reproductive success of paired males with their mate. ESM(x) is directly related to the degree of mate attendance (x) (Figure 2A). The reason is that the more

Table 2.   Predictions of a model of reproductive strategy in ducks based on the degree of stability of the environment during the breeding season.

	Habitat	
	Stable	Variable
Reproductive success (RS)	high	low
Variance in RS	low	high
Forced copulations	rare	frequent*
Cuckoldry	rare	frequent
Mate-guarding	strong	weak
RS with mate (ESM(x)) vs by forced copulations (ESF(x))	ESM(x)>ESF(x)	ESM(x)=ESF(x)

* Under these conditions, males should not only be opportunists but they should actively seek forced copulations.

time a male spends away from his mate, the more the female becomes exposed to forced copulations and harassment by other males. Hence it is more likely that the male may lose his paternity or his mate desert her nest. In more variable environments the probability of nest failure will increase (e.g., because of droughts) and thus the average reproductive success will tend to decrease. The variability in reproductive success will also increase because nest success is usually an "all or nothing" event. This decrease in male reproductive success is illustrated by the slope of ESM(x) which becomes shallower in a more variable habitat.

Males can also sire some offspring through forced copulations. ESF(x) is defined as the average expected reproductive success of paired males with *other* females than their mates. This function is inversely related to the degree of mate attendance (Figure 2B), i.e. as a male spends more time away from his mate, he has more opportunity to engage in forced copulations. The slope of ESM(x) is generally steeper than ESF(x) because the probability of fertilisation for males is higher from within pair copulations than from forced copulations (Burns *et al.* 1980; Cheng *et al.* 1983; Evarts and Williams 1987). The slope of ESF(x) is also shallower in variable habitats for the same reason as in ESM(x).

The total expected reproductive success of males is therefore the summation of ESM(x) and ESF(x). In stable habitats, the probability that a male's mate will produce some offspring is high in most years. Under these conditions, any gain in reproductive success obtained by leaving his mate and actively seeking forced copulations is more than offset by the costs of disturbance to his mate and of being cuckolded. The total expected reproductive success of males (ESM(x) + ESF(x) on Figure 2C) is maximal if they show a high degree of mate guarding, and therefore the model predicts that a mixed reproductive strategy with forced copulation as an alternative mating tactic should *not* evolve in stable habitats. This situation is well illustrated by the Bufflehead, a highly territorial species where forced copulations are absent (Gauthier 1986, 1987c).

In variable and unpredictable habitats, both curves (ESM(x) and ESF(x)) are shallower (Figure 2D). However, and this is the key point, *the ratio of the slope ESM (x)/ ESF(x) decreases,* i.e. the slope of ESM(x) approaches that of ESF(x), as the habitat becomes more variable. The rationale for this is that, in a situation where the risk of nest failure is high, males that inseminate several females instead of only their mate will increase their average reproductive success and reduce its variance. The reduction in variance occurs because nest failure results in the loss of the whole reproductive effort for a bird, but males can increase their chance of producing at least some offspring by inseminating several females. In other words, because the variance of males' expected gain with their mate is high, diversifying their investment will reduce this variance. Recent theoretical models suggest that natural selection may indeed act on variance by favouring strategies with the smallest payoff variance (Gillespie 1977; Rubenstein 1982; Lacey *et al.* 1983). Such models have been loosely termed as bet-hedging strategies. Under these conditions, the total expected reproductive success of males in relation to their degree of mate attendance reaches a maximum before declining (Figure 2D). Therefore, the model predicts that males will persue a mixed reproductive strategy by actively seeking forced copulation and showing a low degree of mate guarding, and hence a loose territorial system will evolve. This situation is well illustrated by the Northern Pintail.

The predictions made by this model (Table 2) agree fairly well with the data available on territorial and mating systems of ducks: strongly territorial species are more abundant in stable environments, forced copulation appears to be a secondary reproductive tactic of paired males, and its frequency is inversely related with the degree of territoriality. Other predictions are also listed, although some of the data required to test them may be difficult to collect in the field (e.g. success of forced copulation). However, the model also predicts that, in highly variable habitats, mate guarding should be weak and territorial behaviour should *not* evolve in monogamous ducks. Therefore, any evidence for that would argue against this model.

Conclusion

It has been shown before that all monogamous species of ducks that are highly territorial are found in relatively stable habitats,

although many other species that occur in similar environments are only weakly territorial (e.g. most of the tribe Aythyini). This suggests that stability of the environment is a necessary but not always sufficient condition to explain the evolution of territoriality and the absence of forced copulations as an alternative mating tactic. In fact, according to the model, any factor that consistently influences the mean and/or variance of male reproductive success could be important. For instance, the potential for renesting or for multiple broods would decrease the variance in male reproductive success in variable habitats. On the other hand, if nest predation is very high in some stable habitats, this should increase the variance. Thus, any factor that increases variance of reproductive success in stable habitats may prevent the evolution of strong territoriality and contribute to maintaining forced copulations as a secondary mating tactic. Clearly, more data are needed adequately to test the predictions of the model and to evaluate the influence of other factors. The study of species using variable habitats should be an especially promising area.

Acknowledgments

Summary

Ducks (sub-family Anatinae) exhibit considerable variability in their degree of territoriality and in the occurrence of extra-pair forced copulations. A model is proposed to explain this variability. Current evidence suggests that territorial behaviour in ducks is closely associated with mate defence. The degree of territoriality is also inversely related to the frequency of forced copulations, and there is good evidence that forced copulation is a secondary mating tactic of paired males and part of a mixed reproductive strategy. Furthermore, strongly territorial species are restricted to stable habitats. Based on this evidence, it is hypothesised that variability in the nesting success of females, and therefore in the expected reproductive success of paired males, determines whether males will engage in a mixed reproductive strategy or exhibit a strong territorial system. In stable habitats, the probability that a male's mate will produce some offspring is high in most years, and males should therefore strongly guard their mate and not actively engage in forced copulation. In variable habitats, the risk of nest failure is high and the variance in male reproductive success will be greater. However, because the variance in male reproductive success will be reduced if they inseminate several females, mate guarding should be weak in these males and they should pursue a mixed reproductive strategy by actively seeking forced copulations.

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Appendix

Territorial system and preferred breeding habitat of 64 of the sub-family Anatinae.

Species	Zoogeography*	Habitat	Type of Territory†	Ref.††
TRIBE TADORNINI				
Tadorna ferruginea	PA	brackish lakes (steppe)	4	10
Tadorna tadornoides	AU	brackish lakes, estuaries	4	32
Tadorna variegata	AU	streams, lakes	4	49
Tadorna tadorna	PA	estuaries, coast	4	30,51
Tadorna radjah	AU	coastal mangroves, mudflats	4	17
TRIBE TACHYERINI				
Tachyeres patachonicus	NO	lakes, estuaries	4	48
Tachyeres pteneres	NO	coast	4	25
Tachyeres brachypterus	NO	coast	4	25
TRIBE CAIRINI				
Cairina moschata	NO	slow-moving rivers, marshes	2	21
Sarkidiornis melanotos	NO/OR/ET	temporary ponds in open woodlands	3	39
Pteronetta hartlaubi	ET	small streams in rain forest	3	22
Nettapus pulchellus	AU	permanent lagoons, lakes (tropical forest)	4	17
Aix sponsa	NA	slow-moving rivers, floodplains	2	20
Aix galericulata	PA	slow-moving rivers, ponds	3	8
Chenonetta jubata	AU	slow-moving rivers, floodplains, swamps	2	24
TRIBE MERGANETTINI				
Merganetta armata	NO	mountain rivers	4	15
TRIBE ANATINI				
Hymenolaimus malacorhynchos	AU	mountain rivers	4	16
Anas waigiuensis	AU	mountain rivers, lakes	4	21
Anas sparsa	ET	fast-flowing rivers	4	4
Anas penelope	PA	ponds, lakes (boreal forest)	2	10
Anas americana	NA/PA	ponds, lakes (parkland)	3	50
Anas falcata	PA	lakes (boreal forest)	2	11
Anas strepera	NA/PA	seasonal ponds (mixed prairie)	2	14,43
Anas crecca	NA/PA	permanent ponds (parkland, boreal forest)	1	28
Anas capensis	ET	shallow ponds, saline pools	2	41
Anas gibberifrons	AU	seasonal lagoons, floodplains	2	18
Anas aucklandica	AU	coastal streams, estuaries	4	46
Anas platyrhynchos	NA/PA	seasonal ponds (mixed prairie, parkland)	2	42,43
Anas rubripes	NA	permanent ponds, coastal marshes	3	36

Anas melleri	ET	streams, forested ponds	3	22
Anas superciliosa	AU	seasonal ponds	2	18
Anas specularis	NO	fast-moving rivers	4	22
Anas specularioides	NO	mountain lakes, coast	4	45
Anas acuta	NA/PA	seasonal ponds (prairie)	1	12
Anas georgica	NO	ponds, lakes, estuaries	2	47
Anas bahamensis	NA/NO	brackish ponds, mangroves	3	27
Anas erythrorhyncha	ET	seasonal ponds, lakes	1	26
Anas hottentota	ET	temporary ponds, marshes	1	9
Anas querquedula	PA	shallow ponds (steppe, forest)	3	10
Anas discors	NA	shallow marshes (prairie, parkland)	3	40,43
Anas cyanoptera	NA/NO	shallow ponds	3	22
Anas smithii	ET	seasonal ponds, marshes	2	37
Anas clypeata	NA/PA	permanent ponds (prairie, parkland)	3	31,35
Marmaronetta angustirostris	PA	alkaline ponds, floodplains	1	10
TRIBE AYTHYINI				
Netta rufina	PA	large alkaline ponds	2	10
Aythya valisineria	NA	lakes, ponds, marshes (parkland)	1	3,22
Aythya ferina	PA	lakes, alkaline marshes (steppe)	2	10
Aythya americana	NA	permanent alkaline lakes	1	22
Aythya collaris	NA	acidic marshes, bogs	2	29
Aythya fuligula	PA	lagoons, deep lakes (boreal forest)	2	10
Aythya affinis	NA	marshes, ponds, lakes (parkland)	1	1,22
TRIBE MERGINI				
Somateria mollissima	NA/PA	coast, estuaries	2	10
Histrionicus histrionicus	NA/PA	mountain rivers	3	6,7
Clangula hyemalis	NA/PA	coast, tundra lakes	3	2
Bucephala albeola	NA	ponds (parkland, boreal forest)	4	13,19
Bucephala islandica	NA/PA	ponds, lakes (parkland, boreal forest)	4	33,34
Bucephala clangula	NA/PA	ponds, lakes (boreal forest)	4	34
Mergus serrator	NA/PA	lakes and streams (forest)	1	10
Mergus merganser	NA/PA	lakes, ponds (boreal forest)	1	10
TRIBE OXYURINI				
Heteronetta atricapilla	NO	permanent marshes	2	44
Oxyura jamaicensis	NA/NO	permanent marshes (parkland)	2	38
Oxyura maccoa	ET	marshes, ponds	4	38
Oxyura australis	AU	permanent marshes	3	22
Biziura lobata	AU	permanent marshes	4	22

* Zoogeographical region inhabited by the species.
NA = Nearctic NO = Neotropical PA = Palearctic ET = Ethiopian OR = Oriental AU = Australian

† See Figure 1 for types of territories

†† References: 1. Afton 1985; 2. Alison 1975; 3. Anderson 1984; 4. Ball *et al.* 1978; 5. Bellrose 1976; 6. Bengston 1966; 7. Bengston 1972; 8. Bruggers 1979; 9. Clark 1971; 10. Cramp and Simmons 1977; 11. Dementiev and Gladkov 1967; 12. Derrickson 1978; 13. Donaghey 1975; 14. Dwyer 1974; 15. Eldridge 1986a; 16. Eldridge 1986b; 17. Frith 1967; 18. Fullagar, P. pers. comm.; 19. Gautier 1987c; 20. Grice and Rogers 1965; 21. Johnsgard 1975; 22. Johnsgard 1978; 23. Kear 1975; 24. Kingsford 1986; 25. Livezey and Humphrey 1985; 26. McKinney 1985; 27. McKinney and Brugger 1979; 28. McKinney and Stolen 1982; 29. Mendall 1958; 30. Patterson 1982; 31. Poston 1974; 32. Riggert 1977; 33. Savard 1982; 34. Savard 1984; 35. Seymour 1974a; 36. Seymour and Titman 1978; 37. Siegfried 1965; 38. Siegfried 1976; 39. Siegfried 1979; 40. Stewart and Titman 1980; 41. Stolen and McKinney 1983; 42. Titman 1983; 43. Titman and Seymour 1981; 44. Weller 1968; 45. Weller 1972; 46. Weller 1975a; 47. Weller 1975b; 48. Weller 1976; 49. Wiliams 1979; 50. Wishart 1983; 51. Young 1970.