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MOVEMENT PATTERNS AND BREEDING CHARACTERISTICS OF ARID ZONE DUCKS

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Most arid zone ducks are nomadic or display a combination of movement patterns. Arid zone ducks that breed in the southern hemisphere (but not those that breed in the northern hemisphere) lay in more months of the year than do non-arid zone ducks. Clutch sizes of ducks that breed in dry environments are higher than those of sedentary ducks that nest in mesic lands, and similar to clutch sizes of migratory ducks that breed in non-arid habitats. Durations of incubation and fledging in arid zone ducks approximate those of sedentary species, but exceed those of annually migratory anatids that breed in mesic lands. Thus, incubation and fledging times in waterfowl that nest in arid country do not conform with the brief periods of flooding of many wetlands in these low rainfall areas.

INTRODUCTION

Waterfowl (Anatidae) breed on and around wetlands in a range of environments, from dry (arid or xeric) to wet (humid or mesic). Most reviews of the breeding biology of waterfowl concentrate on anatids in mesic environments, mainly in North America and western Europe, because the waterfowl in these areas are relatively well studied. This review focuses on a different group of waterfowl, those that breed in arid and semi-arid regions in both hemispheres.

Arid and semi-arid country is characterized by low (<500 mm per year), and variable rainfall (MacLean 1976; West 1983; Evenari 1985). The main arid and semi-arid zones of the world are in northern and southern Africa, western Asia, south-western North America, south-western and north-eastern South America, and central Australia (Bartholomew 1971; MacLean 1976; McGinnies 1979). Xeric lands, although dry for much of the time, often contain large areas of flooded wetlands following local and catchment rainstorms. Considerable numbers of waterbirds feed and breed on these temporary wetlands which form in arid country following heavy rainfalls (Hobbs 1956; Brand 1966; Frith 1967; Uys and MacLeod 1967; Siegfried 1970; Cooper 1974; Geldenuys 1982; Gentilli and Bekle 1983; Maher 1988; Reid 1988; Kingsford 1990; Lawler and Briggs 1991).

The aims of this review are to determine whether movement patterns, number of laying months, clutch and egg sizes, and durations of incubation and fledging of ducks that breed in arid areas differ from those of ducks that breed in non-arid areas. I also consider whether these characteristics in arid zone ducks are related to their breeding hemisphere. The review covers members of the waterfowl tribes Anatini and Aythyini (subfamily Anatinae), and the genera *Stictonetta* and *Malacorhynchus* (respective subfamilies Stictonettinae and Tadorninae) (Livezey 1986); the terms ducks and waterfowl in the review refer to the ducks in these tribes and genera. Arid and xeric include arid and semi-arid lands; humid, non-arid and mesic include humid and subhumid lands. Common and scientific names of species and subspecies of waterfowl follow Johnsgard (1978), except where superceded by Marchant and Higgins (1990).

METHODS

The species and subspecies of ducks were first arranged into categories according to the climate of their breeding habitat (arid or humid). Ducks that generally (= mostly or always) nest in arid or semi-arid areas (all are in the southern hemisphere) were separated from those that sometimes (= partly) nest in arid or semi-arid environments, and the latter group was divided by breeding hemisphere. Mesic zone ducks were first separated according to whether they are sedentary or not. The non-sedentary, or mobile, mesic zone ducks were then classified into two groups according to their movement patterns. Annual (= regular or seasonal) migrants make regular, seasonal migrations to and from their breeding grounds. Partial migrants have irregular, aseasonal movements, or a combination of movement patterns (irregular, regular) and sedentary behaviour, but are not entirely sedentary.

Most of the information on the breeding areas and movement patterns of the waterfowl was obtained from Johnsgard (1978), with supplementary details from the sources listed in the Appendix. The locations of the world's arid and semi-arid zones were ascertained from Bartholomew (1971), MacLean (1976) and McGinnies (1979). Breeding latitudes are the mid-breeding latitudes of the species or subspecies. Laying periods, clutch sizes, and incubation and fledging times were obtained from the sources listed in the Appendix. Laying periods were recorded in units of one month. Clutch sizes, and incubation and fledging times of the species and subspecies, are mean values where provided in the source reference, or midpoints where only a range of figures was available. Egg masses and masses of female waterfowl were obtained from Rohwer (1988). Statistical tests follow Zar (1984); mean data for the groups of waterfowl are reported as ± S.E.

RESULTS

Twenty-eight per cent (22/79) of the ducks included in the review either generally (eight taxa) or sometimes (14 taxa) breed in arid environments, and 72 per cent breed in non-arid or mesic environments. All (8/8) of the ducks that generally nest in arid country have partly or completely irregular modes of movement, and all are austral. Most (11/14) of the ducks that sometimes nest in arid country display a combination of movement types, with 43 per cent (6/14) having some degree of irregular mobility. Seventy-one per cent (10/14) of the partly arid zone ducks are southern breeders. Twenty-nine per cent (23/79) of the ducks included in the review nest in mesic environments and migrate annually to and from their nesting grounds; 11 per cent (9/79) are partial migrants showing a combination of movement patterns; and 32 per cent (25/79) are sedentary in non-arid country. The annual migrants are entirely northern hemisphere species; with one exception, the partial migrants breed in the tropics or southern hemisphere, and the sedentary waterfowl live and breed in both hemispheres.

TABLE 1

Mean ± S.E. (n) mid-breeding latitude (to nearest degree) and mean number of months in which laying has been recorded in the arid and non-arid zone waterfowl listed in the Appendix.

Category of waterfowl	Latitude	Laying months
Arid zone	29 ± 2.1 (22)	9.2 ± 0.9 (21)
Mostly	24 ± 3.0 (8)	12.0 (8)
Partly	31 ± 2.5 (14)	7.5 ± 1.2 (13)
Southern	30 ± 3.5 (10)	9.3 ± 1.3 (9)
Northern	34 ± 3.3 (4)	3.5 ± 0.3 (4)
Non-arid zone		
Annual migrants	52 ± 1.4 (23)	3.4 ± 0.2 (22)
Partial migrants	24 ± 5.6 (9)	4.5 ± 0.8 (6)
Sedentary	23 ± 3.2 (25)	5.8 ± 0.6 (18)

The mean breeding latitude (ignoring hemisphere) of arid zone ducks is lower than the mean breeding latitude of regular migrants, but similar to the mean breeding latitudes of partial migrants and sedentary ducks of mesic areas (Table 1) (ANOVA, $F = 27.3$, $df = 3, 75$, Student-Newman-Keuls test, $P < 0.001$). All the ducks that mostly or always breed in arid lands can lay throughout the year (Table 1). The ducks that sometimes nest in arid lands in the southern hemisphere can also lay over extended periods, but those in northern arid lands do not (Table 1). Compared with annual migrants, sedentary ducks and partial migrants also have long laying periods (Table 1).

Clutch sizes do not differ between ducks that generally nest in arid environments, ducks that sometimes nest in arid austral environments, and ducks that sometimes nest in arid boreal environments (ANOVA, $F = 1.3$, $df = 2, 19$, $P > 0.25$) (Table 2). The mean clutch size of all arid zone nesting ducks is the same as the mean clutch size of annually and partially migrating ducks that breed in mesic environments, but smaller than the mean clutch size of mesic zone, sedentary ducks (ANOVA, $F = 5.7$, $df = 3, 75$, Student-Newman-Keuls test, $P < 0.05$) (Table 2). The mean ratio of egg mass to female mass in arid zone ducks (0.075 ± 0.003, $n = 20$) is similar to the mean egg:

TABLE 2

Mean ± S.E. (n) clutch sizes and incubation periods (days) in the arid and non-arid zone waterfowl listed in the Appendix.

Category of waterfowl	Clutch size	Incubation period
Arid zone	8.6 ± 0.3 (22)	27.0 ± 0.4 (22)
Mostly	8.3 ± 0.4 (8)	27.3 ± 0.6 (8)
Partly	8.8 ± 0.4 (14)	26.9 ± 0.6 (14)
Southern	8.5 ± 0.5 (10)	26.9 ± 0.8 (10)
Northern	9.5 ± 0.5 (4)	26.8 ± 0.5 (4)
Non-arid zone		
Annual migrants	9.1 ± 0.2 (23)	25.1 ± 0.4 (23)
Partial migrants	8.3 ± 0.6 (9)	27.3 ± 0.8 (7)
Sedentary	7.3 ± 0.4 (25)	27.7 ± 0.6 (22)

female mass ratios in non-sedentary ducks in humid areas (annual migrants, 0.072 ± 0.002, n = 22; partial migrants, 0.076 ± 0.005, n = 8). The mean ratio in sedentary, mesic zone ducks is 0.083 ± 0.008 (n = 18).

The mean incubation time of arid zone ducks is similar to the mean incubation times of mesic zone, sedentary ducks and partial migrants (Table 2), but longer than the mean incubation time of mesic zone, annual migrants (ANOVA, $F = 5.1$, df = 3, 70, Student-Newman-Keuls test, $P < 0.05$) (Table 2). Incubation times do not differ between highly arid zone ducks, partly arid zone southern ducks, and partly arid zone northern ducks (ANOVA, $F = 1.0$, df = 2, 19, $P > 0.25$). The limited data available show that ducklings of regular migrants (mesic areas) fledge significantly sooner (7.2 ± 0.3 weeks, n = 19) than the ducklings of both arid zone waterfowl (8.4 ± 0.2 weeks, n = 14) and of sedentary ducks in mesic areas (9.0 ± 0.4 weeks, n = 6) (ANOVA, $F = 7.5$, df = 2, 36, Student-Newman-Keuls test, $P < 0.01$).

DISCUSSION

Few ducks that breed in arid regions are regular migrants or wholly sedentary. Most make irregular movements at times. Such irregular movements, sometimes called nomadism, are common in birds in arid environments. Nomadism is regarded as an adaptation to the unpredictable food resources caused by the variable rainfall in arid and semi-arid lands (Keast and Marshall 1954; MacLean 1976; Davies 1984). Some arid zone ducks display a combination of movement types. They remain on permanent water and may breed there during dry times, but move to ephemerally flooded wetlands to feed and breed when these contain water following rain.

The number of months in which waterfowl lay is related to the seasonality of their breeding environments, and is linked to their movement patterns. Regular migrants breed in highly seasonal environments which are covered in snow and unsuitable for waterfowl in winter. Their reproductive cycles are closely tied to changes in daylength (Murton and Kear 1976; Bluhm 1988; references therein), and they lay for a limited period only. In most of the other ducks considered in this review, laying is less closely linked with photoperiod. Sedentary and partially migratory ducks in non-arid areas have prolonged laying periods, whose durations and timing are often influenced by rainfall as well as by changes in daylength (Weller 1968, 1980; Johnsgard 1978).

Most arid zone waterfowl that breed in the southern hemisphere can lay throughout the year. In these species, nesting is related to a combination of wetland flooding and photoperiod with the effects of the former usually overriding the effects of the latter (Siegfried 1965; Braithwaite and Frith 1969; Braithwaite 1976a, b; Johnsgard 1978; Crome 1986; Halse and Jaensch 1989; Lawler and Briggs 1991; Briggs and Lawler 1991; also see Halse 1985). At least in Australia, arid zone waterfowl rarely breed in years when rainfall is sparse and wetlands are not flooded (Frith 1959; Gentilli and Bekle 1983; Halse and Jaensch 1989; Lawler and Briggs 1991). Laying in Pink-eared Duck *Malacorhynchus membranaceus*, Cape Teal *Anas capensis*, and Grey Teal *Anas gracilis*, is entirely dependent on good rainfall and wetland flooding (Siegfried 1974; Braithwaite 1976a, b; MacLean 1985; Halse and Jaensch 1989). In one of these species, the Pink-eared Duck, males have an unusual testes morphology that permits continuous spermatogenic activity (Braithwaite 1969). This is regarded as an adaptation to the aseasonal and unpredictable availability of the breeding habitats of this species (Braithwaite 1976a).

Arid zone waterfowl breed when wetlands flood because inundation of dry ground enhances production of their food resources, particularly aquatic invertebrates (Frith 1959; Brand 1966; Braithwaite and Frith 1969; Zaloumis and Milstein 1975; Maher and Carpenter 1984; Briggs and Maher 1985; Crome 1986). Food supplies for waterfowl increase in wetlands in both arid and non-arid regions following watering after drying (Kadlec 1962; Krapu 1974; Swanson and Meyer 1977; Van der Valk and Davis 1978; Danell and Sjöberg 1982). However, the effects of wetting and drying on productivity of invertebrates and plants may be more marked in arid environments because of the greater variability in rainfall (Nicholls and Wong 1990), and hence greater areas of ephemeral wetlands in such environments.

The relatively short laying-periods of arid zone, boreal ducks compared with their austral counterparts are probably related to their more seasonal environments, and to the lower variation in annual rainfall in northern arid lands compared with those in the south (Nicholls and Wong 1990). This lower variability in annual rainfall in northern hemisphere, arid country with consequently fewer of the heavy falls of rain required to fill wetlands may also explain the comparatively small number of duck taxa in northern arid lands.

The similar clutch sizes, and egg mass to female body mass ratios, in mobile ducks in both arid and non-arid areas indicate that clutch sizes in arid zone waterfowl are not more limited by low food resources (or other environmental factors) prior to or during laying, than are annual migrants or partially migratory ducks. Soils in arid and semi-arid regions sometimes have lower nutrient levels than soils in humid lands (Jackson 1957; West 1981), although there is considerable variation between continents (Jackson 1957; Stafford Smith and Morton 1990). However, even infertile, arid country can contain wetlands with high nutrient levels because alternating flooding and drying enhance their production and breakdown of organic material, and the turnover of nutrients (Birch 1960; Reddy and Patrick 1975; Cowling 1978; West 1981; Briggs *et al.* 1985). Also, water in arid country carries nutrients into temporarily flooded, run-on areas or wetlands (Stafford Smith and Morton 1990). The clutch sizes of arid zone waterfowl thus appear to be set to the peaks in their food resources that occur after rain fills their wet/dry/wet breeding habitats, rather than to the average availability of food in their breeding wetlands.

The mean incubation and fledging times in arid zone waterfowl are as expected for ducks breeding at their relatively low latitudes. Durations of both incubation and fledging in waterfowl generally decrease as latitude increases (Lack 1968; Johnsgard 1978). The relatively long incubation and fledging periods of arid zone ducks compared with the short incubation and fledging times of regular migrants in non-arid country suggests that wetlands in arid areas are usually flooded long enough for ducks to fledge their young (also see Fullagar *et al.* 1988). However, wetlands in arid country do not always contain water for sufficient time to enable ducklings to fly (Frith 1959; pers. obs.) (see Geldenhuys 1982; Morgan 1982; Goodrick 1984; Williams 1985; Jaensch *et al.* 1988; Maher 1988 for durations of flooding in arid and semi-arid wetlands). Perhaps because of this, arid zone waterfowl appear to breed mainly (but not always) on wetlands that hold water for several months, although they often feed on more ephemeral waters (Maher 1988; Lawler and Briggs 1991). Thus, arid zone waterfowl have not adapted their incubation and fledging times to the short periods of inundation which sometimes occur in the wetlands of their breeding environments.

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APPENDIX

Mid-breeding latitude (°N or °S), movement pattern(s), months in which laying has been recorded, mean or mid clutch size, and incubation (days) and fledging (weeks) times of waterfowl in the tribes of Anatini and Aythyini (subfamily Anatinae) and the genera *Stictonetta* and *Malacorhynchus* (respective subfamilies Stictonettinae and Tadorninae). Data from Middlemiss (1958), Rowan (1963), Frith (1965, 1967), Siegfried (1965, 1974), Weller (1968, 1980), Clark (1969), Lack (1968, 1970), Winterbottom (1974), Kear (1975), Bellrose (1976), Braithwaite (1976a), Murton and Kear (1976), Blake (1977), Cramp (1977), Douthwaite (1977), Skead (1977), Johnsgard (1978), Todd (1979), Weller (1980), Amat (1982), Moulton and Weller (1984), MacLean (1985), Tarsnane (1985), Dumbell (1986), Norman and McKinney (1987), Fullagar *et al.* (1988), MacKinnon (1990), Marchant and Higgins (1990), Lawler and Briggs (1991), Briggs (unpubl. data) and Maher (pers. comm.). The categories of waterfowl (mostly arid zone ducks; partly arid zone ducks; non-arid zone annual migrants; non-arid zone partial migrants; non-arid zone sedentary ducks) are explained in the text.

Category of waterfowl	Latitude	Movement(s)[1]	Laying	Clutch	Incubation	Fledging
Mostly arid zone						
Stictonetta naevosa	30°S	I/S	All months	7	28	9
Malacorhynchus membranaceus	30°S	I	All months	7	26	*
Anas capensis	12°S	I	All months	8	28	7
A. gracilis	30°S	I	All months	8	28	8
A. a. undulata	15°S	S/I	All months	8	29	10
A. erythrorhyncha	18°S	I/S	All months	10	27	8
A. smithii	23°S	S/I/R	All months	9	28	8
A. rhynchotis	35°S	I	All months	9	24	*
Partly arid zone						
A. sibilatrix	45°S	S/R	Aug.–Dec.	7	26	*
A. f. flavirostris	40°S	S/R	Sept.–Dec.	7	24	7
A. platyrhynchos diazi	25°N	S	Apr.–July	9	28	*
A. castanea	35°S	I/S	All months	10	28	8
A. superciliosa rogersi	28°S	I/S	All months	9	29	8
A. v. versicolor	37°S	R/S	*	8	25	*
A. hottentota	17°S	S/I	All months	7	27	9
A. platalea	35°S	R/S	Sept.–Nov.	7	25	*
Chenonetta jubata	30°S	I/S	All months	10	33	8
Marmaronetta angustirostris	37°N	I/S	Apr.–June	11	26	*
Netta rufina	33°N	R/S	Apr.–June	9	27	10
N. erythropthalma brunnea	8°S	S/R	All months	9	27	9
Aythya australis	28°S	I	All months	11	25	*
Aythya nyroca	40°N	R	Apr.–June	9	26	8
Annual migrants						
Aix sponsa	42°N	R	Feb.–July	12	30	9
A. galericulata	45°N	R	Apr.–July	10	29	6
Anas penelope	58°N	R	May–July	9	24	6
A. americana	55°N	R	May–July	8	25	6
A. falcata	62°N	R	May–July	8	25	*
A. strepera	45°N	R	May–July	10	26	8
A. formosa	60°N	R	May–July	8	25	*
A. crecca	56°N	R	March–June	9	22	5
A. p. platyrhynchos	49°N	R	Apr.–July	10	28	8
A. rubripes	47°N	R	Mar.–June	9	27	9
A. a. acuta	58°N	R	Apr.–July	9	22	6
A. querquedula	51°N	R	Apr.–June	9	23	6
A. discors	48°N	R	Apr.–July	10	24	6
A. cyanoptera septentrionalium	40°N	R	Apr.–July	9	23	7
A. clypeata	55°N	R	Apr.–June	9	25	7

Appendix — continued

Category of waterfowl	Latitude	Movement(s)[1]	Laying	Clutch	Incubation	Fledging
Annual migrants — *continued*						
Aythya valisneria	58°N	R	Apr.–May	9	25	9
A. americana	50°N	R	May–July	8	24	9
A. ferina	45°N	R	Apr.–June	8	25	8
A. collaris	52°N	R	May–July	9	26	8
A. baeri	50°N	R	*	8	27	*
A. fuligula	58°N	R	May–Aug.	10	24	7
A. marila	62°N	R	June–July	9	25	*
A. affinis	58°N	R	May–July	10	24	7
Partial migrants						
Nettapus pulchellus	15°S	S/I	Dec.–Mar.	10	*	*
N. coromandelianus	0°	S/I	Dec.–Mar.	8	*	*
N. auritus	0°	S/I	Oct.–May	9	24	9
Anas platyrhynchos maculosa	27°N	S/R	*	10	26	10
A. specularis	46°S	S/R	*	5	30	*
A. s. specularioides	45°S	R/S	Sept.–Nov.	7	30	10
A. georgica spinicauda	27°S	R/S	Aug.–Dec.	7	26	*
Callonetta leucophrys	25°S	R/S	*	9	27	*
Netta peposaca	35°S	R/S	Oct.–Dec.	10	28	*
Sedentary ducks						
Pteronetta hartlaubi	8°N	S	*	9	32	8
Carina moschata	5°S	S	Nov.–June	12	35	*
C. scutulata	7°N	S	*	8	34	*
Anas waigiuensis	5°S	S	May–Jan.	3	28+	8
A. s. sparsa	22°S	S	July–Feb.	6	28	9
A. g. gibberifrons	5°S	S	Apr.–Aug.	9	25	*
Anas gibberifrons albogularis	12°N	S	*	7	24	*
A. a. aucklandica	50°S	S	Oct.–Jan.	4	*	*
A. aucklandica chlorotis	41°S	S	July–Dec.	6	29	8
A. platyrhynchos wyvilliana	20°N	S	All months	8	28	9
A. p. laysanensis	25°N	S	Feb.–July	4	26	*
A. platyrhynchos fulvigula	27°N	S	Feb.–July	10	26	*
A. poecilorhyncha	20°N	S	July–Dec.	8	28	*
A. melleri	20°S	S	July–Sept.	10	28	9
A. pelewensis	5°S	S	*	8	28	*
A. s. superciliosa	45°S	S	Sept.–Dec.	8	28	*
A. luzonica	12°N	S	*	10	26	*
A. acuta eatoni	52°S	S	Nov.–Feb.	5	26	*
A. g. georgica	54°S	S	Oct.–Feb.	5	26	*
A. b. bahamensis	17°N	S	May–Nov.	8	25	*
A. versicolor puna	15°S	S	Nov.–Jan.	6	26	*
Amazonetta brasiliensis	10°S	S	*	7	25	*
Rhodonessa caryophyllacea	30°N	S	May–July	8	*	*
Aythya innotata	20°S	S	Oct.–Jan.	6	27	*
Aythya novae-seelandiae	41°S	S	Oct.–Mar.	7	29	11

[1] I, irregular movements; R, regular movements; S, sedentary; *no data.