MEASURING ANNUAL REPRODUCTIVE SUCCESS, WITH COMMENTS ON THE EVOLUTION OF REPRODUCTIVE BEHAVIOR

BERTRAM G. MURRAY JR.

Department of Biological Sciences, Rutgers University, Piscataway, New Jersey 08855 USA

ABSTRACT.—I present equations for calculating the annual reproductive success (ARS) of females engaged in typically monogamous, rapid double-clutch monogamous, typically polyandrous, and polygynous-polyandrous relationships. With appropriate redefinition of terms, these equations can be used to calculate ARS of males. I calculate annual reproductive success for female Prairie Warblers (*Dendroica discolor*), female Florida Scrub Jays (*Aphelocoma c. coerulescens*), and male and female Spotted Sandpipers (*Actitis macularia*). I show that the ratio of ARS of all females of breeding age to ARS of all males of breeding age equals the sex ratio (all males of breeding age to all females of breeding age).

With data on the Spotted Sandpiper, I illustrate the usefulness of the equations for evaluating hypotheses regarding the evolution of mating systems. Given that a caring parent can rear no more than one brood in a breeding season, and given a low probability of clutch success, I evaluate the potential ARS for hypothetical female Spotted Sandpipers in monogamous, rapid double-clutch monogamous, and polygynous-polyandrous relationships. The maximum ARS is the ARS actually achieved by the Spotted Sandpiper with typical polyandry.

Received 9 April 1990, accepted 28 March 1991.

THE AVERAGE annual reproductive success (ARS) of a group of female birds is the number of offspring produced by that group divided by the number of individuals in the group. The reproductive behavior of birds, however, varies greatly, and reproductive success of females is affected by such factors as clutch size, number of clutches laid, probability of rearing a brood from a clutch, the number of broods reared, and the number of mates obtained.

Most females are monogamous (Lack 1968). Typically, a female mates with one male throughout at least a single reproductive cycle until she is successful or fails. Subsequently, she may make a second effort with the same male, separate and mate with a different male, or cease reproductive activity for the season. In several species, a female may lay two or more clutches in rapid succession (Pitelka et al. 1974; Emlen and Oring 1977; Oring 1982, 1986). In some of these species, the male and female maintain a monogamous pair bond, but each tends a different clutch, as in the Red-legged Partridge (*Alectoris rufa*) (Green 1984). In a few species, such as Temminck's Stint (*Calidris temminckii*) (Hildén 1975), the sexes regularly switch mates between clutches; a female's first mate tends her first clutch, and she usually tends her second. If her second mate accepts responsibility for tending her second clutch, she may obtain a third mate and produce a third clutch. In this system, males often fertilize two clutches, each for a different female, and are thus polygynous. In more typical polyandrous relationships, called "classical polyandry" (Oring 1986), a female switches mates between clutches and the males fertilize only the clutches they are tending (e.g. Spotted Sandpiper, *Actitis macularia*; Hays 1972, Oring and Knudson 1972), or she may mate with several males simultaneously but lay a separate clutch for each of them (e.g. Northern Jacana, *Jacana spinosa*; Jenni and Collier 1972, Jenni 1974).

My purpose is to present equations for calculating the annual reproductive success of females with different reproductive behavior (i.e. monogamy, rapid double-clutch monogamy, polyandry, and polygyny-polyandry) and for evaluating the contributions to reproductive success of clutch size, number of broods attempted, success in rearing broods, and number of mates obtained. With appropriate redefinition of parameters, these equations can be used to calculate reproductive success of males. Furthermore, these equations should allow us to compare ARS of males with ARS of females within and among species more rigorously when evaluating hypotheses accounting for the evolution of reproductive behavior.

MEASUREMENTS OF REPRODUCTIVE SUCCESS

The reproductive success of a female depends on the number of clutches she lays, the number of offspring produced from each clutch, and the number of broods attempted. The number of broods attempted will depend on the length of the breeding season compared with the time required to rear young to independence and on the number of mates she obtains. The numerical value of reproductive success will also depend on whether one counts success in terms of number of broods, fledglings, independent young, or yearlings reared.

In this paper, I present two sets of equations. The first set refers to calculation of ARS in terms of number of broods reared because this measure appears in the denominator of the Murray-Nolan clutch size equation (Murray and Nolan 1989),

$$CS = \frac{a + 1}{\sum_{\alpha}^{\omega} \lambda_x (P_1 + P_2 + \ldots + P_n)}, \quad (1)$$

where CS is the average clutch size, a is the primary sex ratio (males/females), λ_x is the probability that an individual from an egg laid in a successful clutch survives to age class x, α is the average age class of first breeding, ω is the age class of last breeding, P_1 is the probability of rearing a first brood, P_2 is the probability of rearing a second brood, and P_n is the probability of rearing an nth brood. In this equation, ARS is measured as the sum of probabilities of rearing at least one, two, or more broods, that is

$$ARS = P_1 + P_2 + \ldots P_n. \quad (2)$$

This sum of probabilities translates into the average number of broods reared by females. For example, if $P_1 + P_2 + \ldots P_n = 0.77$, then the average female should have reared 0.77 broods per breeding season.

Equation 1 is applicable to either sex. For females, CS refers to the number of eggs laid in a clutch; for males, CS refers to the number of eggs fertilized in a clutch. Note that the average clutch size should be identical for males and females in the same population. Thus, differences between the sexes in one parameter (e.g. survivorship, age of first breeding, or probabilities of rearing one, two, or more broods successfully) should be balanced by differences in one or more of the other parameters.

The second set of equations is presented because ornithologists normally measure reproductive success in terms of the number of offspring produced.

The equations for ARS vary with the mating system, the number of broods or offspring reared, and whether success is counted through rearing young to fledging, independence, or some other stage. Thus, the notation of ARS requires elaboration. For example, ARS(m, b, i) would refer to the annual reproductive success of monogamous (m) females rearing broods (b) through independence (i). Other specific definitions are introduced at the appropriate places below. The form of the equations does not differ with regard to whether success is counted through nest-leaving, fledging, independence, or some other stage. Thus, the third letter modifying ARS only indicates the stage through which success is counted. In these equations, I use success through independence because I think this is probably most important (Murray and Nolan 1989). Often, investigators are unable to obtain such data, and they may wish to measure success through nest-leaving. The equation is the same, but ARS would have a different modifier. Thus, ARS(m, b, nl) refers to the annual reproductive success of monogamous females rearing broods through nest-leaving. Furthermore, the reader should be aware that the equations presented below do not represent an exhaustive list that accounts for all of the variations in reproductive behavior. Some of these variations will be mentioned below.

Finally, it should be emphasized that female (or male) ARS refers to the success of all the females (or males) in the breeding population, which is defined as all females (or males) of breeding age, including experienced but nonbreeding "loafers" and excluding inexperienced birds that are not breeding and have never made a breeding attempt. To account for nonbreeding experienced birds, I use the parameter Q, which is the proportion of the breeding population of females (or males) that actually breed.

EQUATIONS FOR CALCULATING ANNUAL REPRODUCTIVE SUCCESS

Monogamy.—Typically, a monogamous female lays a clutch of eggs and tends it, with or without assistance from her mate, until she either successfully rears her brood or fails. In some species, one or the other member of the pair may desert before the young reach independence. Often no more than a single brood can be reared during a breeding season because the time required for development of the young to independence precludes rearing two. If development time of young is short relative to the length of the breeding season, more than one brood may be reared. After either success or failure of a nesting attempt, a female (if she has time) may attempt a second brood with her first mate or she may mate with a different male. The ARS for monogamous (m) females in terms of number of successful broods (at least one young reared to independence) is

$$\mathrm{ARS(m, b, i)} = Q \sum c_n s_n, \tag{3}$$

where c_n is the average number of clutches laid per female in producing brood n to independence, and s_n is the probability of a brood n clutch producing at least one young to independence, regardless of whether or not the mate is the same male for each clutch, and n refers to the first, second, or later brood.

The ARS of monogamous (m) females in terms of the number of young (k) reared to independence (i) is

$$\mathrm{ARS(m, k, i)} = Q \sum c_n s_n k_n, \tag{4}$$

where k_n is the average number of young reared per successful brood n.

Rapid double-clutch monogamy.—If development time is long relative to the length of the breeding season, monogamous females, as described above, can produce no more than one brood during a breeding season. A pair-bonded monogamous female of a species whose young have a long development time may improve her reproductive success during a breeding season if she rapidly lays two clutches, one to be tended by her mate, the other by herself. The success of this behavior depends on the ability of a lone parent to rear a brood successfully. The maximum number of broods that can be reared by a female and her mate with rapid double-clutch monogamy is two, one by each member of the pair. Because replacing failed clutches is still a possibility, the annual reproductive success in terms of broods reared to independence of double-clutch monogamous (dcm) females is

$$\mathrm{ARS(dcm, b, i)} = Q(c_m s_m + c_f s_f), \tag{5}$$

where c_m and c_f are the average number of clutches tended by males and females, respectively, and s_m and s_f are the probabilities that a clutch tended by a lone male or female, respectively, will produce young to independence.

The ARS of rapid double-clutching females in terms of young reared to independence is

$$\mathrm{ARS(dcm, k, i)} = Q(c_m s_m k_m + c_f s_f k_f), \tag{6}$$

where k_m and k_f are the average number of young reared per successful clutch tended by a male or a female, respectively.

Classical polyandry.—Rarely, females may obtain more than one mate. In species such as the Spotted Sandpiper, females often desert their mates. The males care for the eggs and young, and the females obtain additional mates. In species such as the Northern Jacana (Jenni and Collier 1972, Jenni 1974), a female may copulate with several mates on a single day, but lay a separate clutch for each of them. If the caring parent can rear no more than one brood, the maximum number of broods a female can produce is the number of mates she is able to obtain.

In classical polyandry (pa), the females' ARS in terms of broods reared through independence is given by

$$\mathrm{ARS(pa, b, i)} = Q \sum_{g=1} \left(F_g \sum_{r=1} c_r s_r \right), \tag{7}$$

where F_g is the frequency of females mated to g number of mates, c_r is the average number of clutches laid for the rth mate, and s_r is the probability that a clutch laid for the rth mate is successful. In terms of number of independent young reared, the ARS is

$$\mathrm{ARS(pa, k, i)} = Q \sum_{g=1} \left(F_g \sum_{r=1} c_r s_r k_r \right), \tag{8}$$

where k_r is the mean number of fledglings per successful clutch of the rth mate.

Cooperative polyandry.—In species with cooperative polyandry, such as the Galapagos Hawk (*Buteo galapagoensis*), two or more males and a female form a group that attends one clutch or brood at a time (Faaborg and Patterson 1981). The calculation of ARS for females is no different from that for monogamous females. Thus, Eqs. 3 and 4 are appropriate for calculating ARS for females that participate in cooperative polyandrous systems.

Polygyny-polyandry.—In some species, both sexes may have more than one mate. In the Temminck's Stint, for example, after a female lays her first clutch, she leaves her mate, but he delays incubation and solicits a second female. The female tends her second clutch, unless her second mate does, in which case she solicits a third male. In any case, she tends her final clutch alone. Although an individual, as the lone caring parent, can rear only one brood during a breeding season, each male and female may be the genetic parent of more than one brood. In polygynous-polyandrous systems the success of females in *rearing* young must be added to the success of their mates. Thus, the ARS for females in polygynous-polyandrous (pp) systems in terms of broods reared to independence is

$$\text{ARS(pp, b, i)} = Q \sum_{g=1} \left(F_g \sum_{r=1} c_r s_r \right) + c_f s_f \qquad (9)$$

or, in terms of young reared,

$$\text{ARS(pp, k, i)} = Q \sum_{g=1} \left(F_g \sum_{r=1} c_r s_r k_r \right) + c_f s_f k_f . \qquad (10)$$

In some polygynous-polyandrous species, such as the Greater Rhea (*Rhea americana*), a group of females visits individual males in sequence and provides each with a clutch (Bruning 1975). Females do not incubate eggs or rear young. Equations 7 and 8 are appropriate for females participating in this kind of polygynous-polyandrous system.

ILLUSTRATIONS WITH FIELD DATA

Despite a voluminous literature reporting "hatching success," "fledging success," or "nesting success," there are few published field data adequate for performing computations of ARS as proposed here. Indeed, until recently (e.g. Oring et al. 1983, Woolfenden and Fitzpatrick 1984, Grant and Grant 1989, and individual papers in Clutton-Brock 1988 and Newton 1989), few studies have reported the number of young reared per female during a breeding season. Even fewer studies have reported either the number of clutches laid per brood (c_n) or the probability that a brood n clutch will be successful (s_n).

We have available for analysis only two published studies of monogamous species (i.e. Prairie Warbler, *Dendroica discolor*, and Florida Scrub Jay, *Aphelocoma c. coerulescens*) that provide sufficient data for illustrative purposes. In addition, Lew Oring has generously provided me with data from his study of the polyandrous Spotted Sandpiper. There are no adequate data for rapid double-clutch monogamous females or for females in polygynous-polyandrous systems.

Prairie Warbler.—For monogamous species, ARS is calculated with Eq. 3 or 4. In a sample of 70 female Prairie Warblers (Nolan 1978), followed throughout most of a breeding season, 49 successfully reared one brood and 5 reared a second brood through nest-leaving (nl). In the rearing of the 49 first broods, 203 clutches were laid (Murray and Nolan 1989). Thus, c_1, the number of clutches laid per female in producing a first brood, is 203/70 = 2.900, and s_1 is 49/203 = 0.241. In rearing 5 second broods, 15 additional clutches were laid (Murray and Nolan 1989). Thus, c_2, the average number of clutches laid per female in producing a second brood, is 15/70 = 0.214, and s_2 is 5/15 = 0.333. The ARS(m, b, nl) of female Prairie Warblers is $c_1s_1 + c_2s_2 = (2.900 \times 0.241) + (0.214 \times 0.333) = 0.770$. This means that the probability of successful reproduction is 0.770. Alternatively, one could say that on average females produce 0.770 successful broods in a breeding season.

Murray and Nolan (1989) measured ARS with Eq. 2. Of the 70 females, 49 reared at least one brood and 5 reared two broods successfully through nest-leaving (Murray and Nolan 1989). Thus, P_1, the probability of rearing at least one brood, is 49/70 = 0.700, and P_2, the probability of rearing two broods, is 5/70 = 0.071; $P_1 + P_2 = 0.771$. Because P_n and c_ns_n are mathematically equivalent, ARS $= P_1 + P_2 + \ldots P_n = c_1s_1 + c_2s_2 + \ldots c_ns_n$.

Florida Scrub Jay.—Murray et al. (1989) presented similar data for 495 breeding female seasons of 143 female Florida Scrub Jays. The number of first-brood clutches per female per year was 644/495 = 1.301, and the number of second-brood clutches per breeding female per year was 33/495 = 0.0667. The probability of success (through nest-leaving) of first brood clutches was 348/644 = 0.5404, and of second brood clutches, 16/33 = 0.4848. Thus, ARS(m, b, nl) is $(1.3010 \times 0.5404) + (0.0667 \times 0.4848) = 0.7031 + 0.0323 = 0.7354$. Murray et al. (1989) calculated $P_1 + P_2 = 348/495 + 16/495 = 0.7030 + 0.0323 = 0.7353$ for the reproductive success through nest-leaving of the Florida Scrub Jay.

TABLE 1. Breeding success of female Spotted Sandpipers engaged in different mating relationships. C is the number of clutches laid. S is the number of clutches producing at least one fledgling. F is the number of fledglings reared.

Clutch number	First Mate			Second Mate			Third Mate			Fourth Mate		
	C	S	F	C	S	F	C	S	F	C	S	F
	Monogamous Females ($F_1 = 0.4587$)											
1	100	31	88									
2	32	9	18									
3	17	6	19									
4	4	0	0									
5	2	1	2									
	155	47	127									

ARS(broods, monogamous females) = c_1s_1 = (155/100)(47/155) = 0.4700

ARS(fledglings, monogamous females) = $c_1s_1k_1$ = (155/100)(47/155)(127/47) = 1.2700

Clutch number	First Mate			Second Mate			Third Mate			Fourth Mate		
	C	S	F	C	S	F	C	S	F	C	S	F
	Bigamous Females ($F_2 = 0.3532$)											
1	77	26	73	—	—							
2	11	7	15	66	25	84						
3	1	1	2	24	9	29						
4				5	1	1						
5				1	1	3						
	89	34	90	96	36	117						

ARS(broods, bigamous females) = $c_1s_1 + c_2s_2$ = (89/77)(34/89) + (96/77)(36/96) = 0.9091

ARS(fledglings, bigamous females) = $c_1s_1k_1 + c_2s_2k_2$ = (89/77)(34/89)(90/34) + (96/77)(36/96)(117/36) = 2.6883

Clutch number	First Mate			Second Mate			Third Mate			Fourth Mate		
	C	S	F	C	S	F	C	S	F	C	S	F
	Trigamous Females ($F_3 = 0.1697$)											
1	37	5	12	—	—	—	—	—	—			
2	8	1	3	29	14	41	—	—	—			
3	2	1	4	8	3	8	27	8	22			
4				2	2	4	12	3	5			
5							3	1	2			
	47	7	19	39	19	53	42	12	29			

ARS(broods, trigamous females) = $c_1s_1 + c_2s_2 + c_3s_3$ = (47/37)(7/47) + (39/37)(19/39) + (42/37)(12/42) = 1.0270

ARS(fledglings, trigamous females) = $c_1s_1k_1 + c_2s_2k_2 + c_3s_3k_3$ = (47/37)(7/47)(19/7) + (39/37)(19/39)(53/19) + (42/37)(12/42)(29/12) = 2.7297

Clutch number	First Mate			Second Mate			Third Mate			Fourth Mate		
	C	S	F	C	S	F	C	S	F	C	S	F
	Quadrigamous Females ($F_4 = 0.0183$)											
1	4	0	0	—	—	—	—	—	—	—	—	—
2	2	1	2	2	0	0	—	—	—	—	—	—
3				2	1	4	2	0	0	—	—	—
4							2	0	0	2	2	3
5										2	0	0
	6	1	2	4	1	4	4	0	0	4	2	3

ARS(broods, quadrigamous females) = $c_1s_1 + c_2s_2 + c_3s_3 + c_4s_4$ = (6/4)(1/6) + (4/4)(1/4) + (4/4)(0/4) + (4/4)(2/4) = 1.0000

ARS(fledglings, quadrigamous females) = $c_1s_1k_1 + c_2s_2k_2 + c_3s_3k_3 + c_4s_4k_4$ = (6/4)(1/6)(2/1) + (4/4)(1/4)(4/1) + (4/4)(0/4)(0/0) + (4/4)(2/4)(3/2) = 2.2500

$$\text{ARS(pa, b, f)} = Q \sum_{g=1} (F_g \sum_{r=1} c_r s_r) = 0.7293$$

$$\text{ARS(pa, k, f)} = Q \sum_{g=1} (F_g \sum_{r=1} c_r s_r k_r) = 2.0365$$

TABLE 2. Breeding success of male Spotted Sandpipers mated to monogamous, bigamous, trigamous, and quadrigamous females. C is the number of clutches laid. S is the number of clutches producing at least one fledgling. F is the number of fledglings reared.

	Mates														
Clutch number	Monogamous			Bigamous			Trigamous			Quadrigamous			All males		
	C	S	F	C	S	F	C	S	F	C	S	F	C	S	F
1	92	31	88	130	48	151	77	25	67	14	2	6	313	106	312
2	36	7	14	43	17	47	40	10	27	4	2	3	123	36	91
3	19	6	19	11	5	9	8	3	7	0	0	0	38	14	35
4	6	2	4	1	0	0	2	0	0	0	0	0	9	2	4
5	2	1	2	0	0	0	1	0	0	0	0	0	3	1	2
	155	47	127	185	70	207	128	38	101	18	4	9	486	159	444
c_1		1.6848			1.4321			1.6623			1.2857			1.5527	
p_1		0.3032			0.3784			0.2969			0.2222			0.3272	
k_1		2.7021			2.9571			2.6579			2.2500			2.7924	
c_1p_1		0.5108			0.5419			0.4935			0.2857			0.5080	
$c_1p_1k_1$		1.3803			1.6025			1.3118			0.6428			1.4187	

Spotted Sandpiper.—The Spotted Sandpiper is a typically polyandrous species. A female often switches mates between laying clutches (Oring 1986). For calculating ARS, Eqs. 7 and 8 are appropriate. The Spotted Sandpiper has been studied in detail, and reproductive data were reported in Oring (1982) and Oring et al. (1983). In the following analysis, I have used Oring's data from 1973 through 1989 (except 1984 and 1985, when female reproduction was experimentally interrupted).

Females may lay up to five clutches for one, two, three, or four males (Table 1). Annual reproductive success is calculated for monogamous, bigamous, trigamous, and quadrigamous females separately and, then, for all females with Eq. 7 (Table 1). The ARS(pa, b, f) is 0.7293.

The number of fledglings produced per successful brood varied with clutch sequence number and the number of males per female (Table 1). From Eq. 7, ARS(pa, k, f) for all females is 2.0 (Table 1). The ARS(pa, k, f) can be calculated separately for females with different numbers of mates. It is 1.27 for monogamous females, 2.69 for bigamous females, 2.73 for trigamous females, and 2.25 for quadrigamous females (calculated from data in Table 1).

I have used Eq. 3 to calculate ARS(m, b, f) for male Spotted Sandpipers mated to monogamous, bigamous, trigamous, and quadrigamous females, separately, and for all males (Table 2). Males mated to bigamous females were most successful, and males mated to quadrigamous females were least successful. Inasmuch as quadrigamy occurred in breeding seasons characterized by high rates of clutch loss, the low success of males mated to quadrigamous females may have been a seasonal effect rather than an effect of its mate being quadrigamous. Indeed, trigamy and quadrigamy may be a consequence of high nest failure in bad years, which makes more males available to females for a third or fourth breeding attempt. If there were high nest success and if the sex ratio were 1.4, few females could obtain even two mates. The overall ARS(m, b, f) for males is 0.5080.

Finally, consider the ratio of the ARS of females of the breeding population to the ARS of males of the breeding population. For the Spotted Sandpiper, ARS(pa, b, f)/ARS(m, b, f) = 0.7293/0.5080 = 1.44, and ARS(pa, k, f)/ARS(m, k, f) = 2.0365/1.4187 = 1.44. This is the sex ratio (males/females) of the breeding population (i.e. 313/218).

DISCUSSION

The evolution of reproductive behavior.—Several factors constrain successful reproduction. One constraint is the availability of mates. In my hypothetico-deductive theory on the evolution of mating systems (Murray 1984, 1985b), I argued that males and females shared mates (forming polyandrous and polygynous relationships, respectively) when the availability of mates was limited and individuals could not afford to wait for a monogamous relationship. Waiting always results in increasing the annual replacement fecundity. If the annual replacement fecundity were greater than the number of eggs that a female could lay or a male fertilize in monogamous relationships during a breeding season, then polygyny or polyandry should evolve.

A second constraint is the loss of eggs or young in nests, mainly to predation and inclement weather. Although there is ample time for rearing two broods during a breeding season in the Prairie Warbler, only 70% of females rear even one because of high rates of predation on eggs and young in the nest (Nolan 1978, Murray and Nolan 1989). Female Prairie Warblers may lay up to seven clutches in a breeding season. If the breeding season were longer, more clutches could be laid (higher c_n) in producing a successful brood, and we might expect a higher ARS; if shorter, we might expect a lower c_n and lower ARS.

A third constraint is the length of the breeding season relative to the length of time required to rear independent young. I have discussed this constraint with regard to the evolution of clutch size (Murray 1979, 1985a, 1991). Here, I want to address this constraint with regard to the evolution of mating systems.

If the time required to rear independent young is short relative to the length of the breeding season, then monogamous pairs can rear more than one brood in a breeding season. If it is long, then no more than one brood can be reared by a pair in a typical monogamous relationship. If it is long, however, more than one brood could be reared if each parent cared for one clutch and brood (rapid double-clutch monogamy) or if one or both parents obtained more than one mate (polygamy). Let us now examine the possibilities open to female Spotted Sandpipers by applying the ARS equations to empirically determined constraints on Spotted Sandpiper reproduction.

The constraints on Spotted Sandpiper reproduction are (1) that the time required to rear a brood successfully, relative to the length of the breeding season, precludes a second successful attempt by the parent caring for the eggs and young and (2) that the probability of nest success (s_n) is 0.327 (i.e. 159 successes/486 clutches; Table 1). Given these constraints, female Spotted Sandpipers achieve an empirically determined ARS(pa, b, f) of 0.729 (Table 1). We may now consider whether it is possible for female Spotted Sandpipers to achieve an ARS of 0.729 broods as typically monogamous females, as rapid double-clutch monogamous females, or as polyandrous females mated to polygynous males.

First consider typical monogamy. To achieve an ARS(m, b, f) of 0.729, the *average* female would have to lay 2.23 clutches during the breeding season (Eq. 3). Whereas some females may be successful with their first clutch, others could be unsuccessful with their first, second, third, and fourth. We want to know the expected success of the *average* monogamous female Spotted Sandpiper during an egg-laying period in Minnesota, which varies among years from 34 to 48 days (mean = 42.2; Lank et al. 1985). Considering the length of incubation (ca. 21 days), the length of time from hatching to fledging (14–18 days), the time between failure and completion of the next clutch (8–10 days; Lank et al. 1985), and the fact that many females do not arrive at the beginning of the egg-laying period (Oring et al. 1983, Lank et al. 1985), it seems unlikely that the *average* monogamous female Spotted Sandpiper could produce as many as two clutches (even as failures) per season. In fact, the average monogamous female Spotted Sandpiper lays only 1.55 clutches (i.e. 155/100; Table 1), owing in part to the later arrival of the females that are monogamous. Seemingly, typical monogamy seems a poor alternative to polyandry for the Spotted Sandpiper. Of course, a pair of Spotted Sandpipers together might have greater success rearing a brood than either male or female as a single parent (i.e. s_1 in Eq. 3 could be >0.327). In fact, lone males are more successful than males assisted by mates (Oring et al. 1983, Oring pers. comm.). Typical monogamy does not seem to be an option open to female Spotted Sandpipers.

Perhaps, our hypothetical Spotted Sandpiper could increase its probability of success by engaging in rapid double-clutch monogamy. Assuming that the probability of success for clutches reared by either a male or female is 0.327, we can determine (Eq. 5) that the average female would still have to lay 2.23 clutches if it were to achieve an ARS(dcm, b, f) of 0.729. Conceivably, females could do this during the 34 to 48-day egg-laying period. On average, only 23% of females would have to lay one replacement clutch (i.e. a total of three clutches). One constraint on success would be how readily an incubating or brooding male or female could be seduced into courtship by its mate for the laying of the replacement clutch. In the Red-legged Partridge (the best known rapid double-clutching monogamous species), females lay a replacement clutch only if a clutch is lost before incubation starts. Once incubation starts, replacement of a lost clutch can occur only after both mates fail (with $s_1 = 0.327$, the probability of both failing is 0.107). Furthermore, few yearling females laid two clutches, and only 60–80% of experienced females attempted two clutches (Green 1984). Thus, on average, female Red-legged Partridges lay fewer than two clutches per season. If the same behavioral restrictions were placed on female Spotted Sandpipers, they could not reproduce as well with rapid double-clutch monogamy as they do with typical polyandry.

A second problem, the effect of the sex ratio, is probably more serious. If clutches and broods could be successfully tended by one parent, as in rapid double-clutch monogamy, and if one sex significantly outnumbered the other, it is unclear why members of the rarer sex should maintain pair bonds at all. Seemingly, if males were the more numerous sex, females could do better by courting additional mates rather than by maintaining monogamous pair bonds. If this were so, then rapid double-clutch monogamy should be limited to species in which the numbers of males and females were about equal. It seems not coincidental that in the only species for which we have good information, the Red-legged Partridge, the sex ratio is near unity (Green 1984). When the sex ratio is near unity, an individual improves its chance of producing two broods by maintaining the pair bond because, if it deserted, the probability of finding a second mate would be low. If, on the other hand, males outnumbered females, and males alone could successfully rear young, then polyandry should be expected.

The monogamous male-polyandrous female relationships, characteristic of the Spotted Sandpiper, could occur only if single-brooded males were reproducing at least at the replacement rate. If single-brooded males were not replacing themselves, then their multibrooded females could not be replacing themselves either (Murray 1984, 1990).

If male mortality were sufficiently high, males would have to have a greater clutch size, earlier age of first breeding, a greater probability of rearing one, two, or more broods, or some combination of these than with lower mortality (Eq. 1). Given the constraints listed above, males would have to be multibrooded, increasing their P_2. Males could do this either by rapid double-clutch monogamy or by obtaining additional mates. But, if males outnumber females, and if females desert their mates and are polyandrous, precluding rapid double-clutch monogamy, it is difficult to see how males could be multibrooded. They could possibly postpone incubation of the first clutch and solicit second females, as occurs in the Temminck's Stint (Hildén 1975). After the male Temminck's Stint fertilizes his second female's eggs, he incubates his first clutch, leaving the second clutch for the female to incubate. If a female's second mate is mating for the first time, she may desert him and solicit a third mate. In such a system, males have a chance to produce two broods, one by each of two females, and females could produce two or more broods, each fertilized by a different male.

The demography of polygynous-polyandrous systems (such as those of the Temminck's Stint, Greater Rhea, and some of the tinamous) and rapid double-clutch monogamous systems (such as that of the Red-legged Partridge) has not been described sufficiently well (or at all) to test these interpretations of the possible cause-and-effect relationships between demographic parameters and mating relationships. Nevertheless, we know that rapid double-clutch monogamy and polygyny-polyandry occur, and it seems worthwhile to propose what the demography of species engaged in these different mating systems might be.

Assuming that the primary sex ratio remains constant, Eq. 1 indicates that an increase in mortality must be balanced by an increase in clutch size, an earlier age of first breeding, an increase in successfully rearing a first brood (P_1), an increase in successfully rearing additional broods (P_2, P_3, etc.), or some combination of these. In some species (such as in many Galliformes, ratites, and other ground living forms), the evolutionary response to high mortality is larger clutches or an early age of first breeding, or both. But, in shorebirds the evolutionary response seems to have been an increase in the number of broods reared. The only way to increase the number of broods reared, if a brood-tending parent is limited to one successful brood per year, is for each member of a pair to care for a separate brood (rapid double-clutch monogamy) or for individuals to obtain additional

TABLE 3. Relationship between relative survivorship, sex ratio, and mating relationship of males and females ("high," "moderate," and "low" are relative rates) when the clutch and brood caring parent is limited to successfully rearing no more than one brood per year. When annual survivorship is either "moderate" or "low" a maximum of one brood per year is not sufficient to assure replacement.

Mode of reproduction	Relative annual survivorship		Sex ratio
	Males	Females	
Monogamy	"high"	"high"	≈1
Rapid double-clutch monogamy	"moderate"	"moderate"	≈1
Polyandry	"high"	"low"	≫1
Polygyny-polyandry	"moderate"	"low"	>1

mates that accept rearing the offspring with little or no help (polygamy). Which of these possible mating relationships occurs seems to be a function of the absolute and relative survivorship of males and females (Table 3).

Seemingly, for any set of circumstances (e.g. survivorship of males and females, age of first breeding, length of time required to rear young to independence relative to the length of the breeding season, and the probability of rearing young from a clutch), there seems to be only one combination of features (e.g. clutch size, mating system) that could prevail in a "steady-state" population (one whose numbers are fluctuating about a mean value). These combinations are those expected from my hypothetico-deductive theories on the evolution of clutch size (Murray 1979, 1985b, 1991) and mating systems (Murray 1984, 1985a). Unfortunately, quality demographic data are scarce. Nevertheless, the general pattern of relationships predicted by the theories are those that are observed (Murray 1979, 1984, 1985a, b, 1991).

With regard to the evolution of polyandry in the Spotted Sandpiper, comparative data on its close relative, the Common Sandpiper (*Actitis hypoleucos*), which is monogamous (Holland et al. 1982), would be useful. What is known is suggestive. The Common Sandpiper has a relatively high adult survivorship (ca. 90%; Holland et al. 1982) compared with annual return rates of 60% for experienced females and 62% for experienced males in the Spotted Sandpiper (Oring et al. 1983). Furthermore, the Common Sandpiper has a much higher survival of clutches through hatching (80–84%; Cramp et al. 1983) and through fledging (ca. 35%; Holland et al. 1982), than the Spotted Sandpiper has (44% through hatching and 22.4% through fledging; Oring et al. 1983). Both high survivorship through hatching and fledging (i.e. high P_1) and high annual adult survivorship tend to favor monogamy (Table 3). More accurately, the absence of high mortality at these stages does not enhance selection for multibroodedness or polyandry (Murray 1984).

Alternative hypotheses.—The alternative hypotheses proposed to account for classical polyandry in birds (reviewed by Oring 1986) are nonquantitative, often conflicting, and difficult to test. The equations I offer here should be useful in sorting out the many ideas proposed to account for the various mating relationships. For example, the equations and analysis support the views that (1) a sex ratio that favors males is a precondition for the evolution of polyandry (Maynard Smith and Ridpath 1972), (2) "classical" polyandry is favored when females must produce many eggs because of high predation rates on clutches (Jenni 1974; Oring 1982, 1986), and (3) polygyny-polyandry (what Oring calls "multi-clutch polygamy") is not an evolutionary stage between monogamy and polyandry (Oring 1982, 1986). These ad hoc hypotheses are consistent with my general theory on the evolution of mating systems (Murray 1984, 1985a).

Most discussions regarding the evolution of polyandry refer to such factors as the availability of resources (mainly food) in time and space, relative efficiency of males and females in coping with uniparental care, genetic relatedness of the individuals sharing a mate, and relative abilities of males and females in assessing alternative reproductive opportunities (reviewed by Oring 1986). Although some of these factors may be necessary conditions for the evolution of polyandry, such as successful uniparental care, none of them is a sufficient condition, and others may be neither necessary nor sufficient. For example, for uniparental male care and polyandry to evolve, it is not necessary for uniparental male care to be more successful, or even as successful, as biparental care or even uniparental female care. It is only necessary that a female be able to rear more offspring with two or more males than she could as a monogamous female. If she were to participate in parenting because she was the better parent, she would be unable to replace herself. Thus, failure to desert her mate and court additional males would result in extinction. Furthermore, if food resources precluded successful uniparental rearing of young, or if the sex ratio did not favor males, the population would also become extinct. Thus, polyandry is found in species in which males outnumber females and males are able to rear the young unaided (Murray 1984).

The need for reporting the new demographic parameters.—As indicated above, ARS $= P_1 + P_2 + \ldots P_n = c_1s_1 + c_2s_2 + \ldots c_ns_n$. Unfortunately, the values for these parameters are not extractable from the data reported in the literature. The usual report on reproductive success provides data on clutch size, the number of clutches started, the fraction of eggs that hatch or of clutches that produce hatchlings, and the fraction of hatchlings that survive to fledging or the fraction of clutches that produce fledglings. Increasingly, with long-term studies of distinctively marked individuals, the average number of young (e.g. fledglings, yearlings, or breeders) per female (or pair) is reported (e.g. studies in Clutton-Brock 1988, Newton 1989). Nevertheless, despite the seeming fullness of the reported data, none of the parameters of the ARS equations can be determined from them.

Measuring ARS rather than clutch (or egg) success and measuring ARS in terms of broods reared rather than young reared are essential for comparing reproductive success within, between, and among populations (Murray 1991). For example, I have proposed that small clutch sizes occur in the tropics because the females' probabilities of rearing one, two, or more broods are greater there than at higher latitudes (Murray 1991). Even though the probability of success of a clutch (s_n) is low in the tropics, the number of clutches started (c_n) for each brood and the average number of broods reared could be larger than in temperate regions, because of the longer breeding season in the tropics, resulting in a greater ARS(broods) (i.e. $P_1 + P_2 + \ldots P_n$). If ARS(broods) is greater in the tropics than at higher latitudes, then clutch sizes should be smaller in the tropics (Eq. 1).

In the only comparison with fairly good data that I have found, the House Sparrow (*Passer domesticus*) has longer breeding seasons and more but smaller clutches at lower latitudes than at higher latitudes (Summers-Smith 1988). The effect of a larger clutch size on reproductive success at higher latitudes is offset by the shorter breeding season and fewer clutches laid there, such that the average number of fledglings produced per pair per year is virtually the same at all latitudes. Although ARS in terms of broods is greater in the tropics, ARS in terms of fledglings reared is approximately the same in tropical and temperate regions.

As a result of this analysis, I urge that the number of clutches started of first, second, and later broods (c_1, c_2, etc.) and the probabilities of first, second, and later brood clutches (s_1, s_2, etc.) successfully producing young to nest-leaving, if not independence, be reported in future studies (for examples, see table 2 in Murray and Nolan [1989], table 3 in Murray et al. [1989], and Table 1 in this paper).

ACKNOWLEDGMENTS

I am most grateful to Lewis W. Oring who generously allowed me to examine his data on the Spotted Sandpiper and permitted me to report the results of my analysis. I thank David J. T. Hussell, L. W. Oring, and William M. Shields for commenting on earlier drafts of the manuscript.

LITERATURE CITED

BRUNING, D. F. 1975. Social structure and reproductive behavior in the Greater Rhea. Living Bird 13: 251–294.

CLUTTON-BROCK, T. H. (Ed.). 1988. Reproductive success. Chicago, Univ. Chicago Press.

CRAMP, S., ET AL. (Eds.) 1983. Handbook of the birds of Europe, the Middle East, and North Africa, vol. III. Oxford, Oxford Univ. Press.

EMLEN, S. T., & L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 187: 215–223.

FAABORG, J., & C. B. PATTERSON. 1981. The characteristics and occurrence of cooperative polyandry. Ibis 123: 477–484.

GRANT, B. R., & P. R. GRANT. 1989. Evolutionary dynamics of a natural population: the Large Cactus Finch of the Galápagos. Chicago, Univ. Chicago Press.

GREEN, R. E. 1984. Double nesting in the Red-legged Partridge *Alectoris rufa*. Ibis 126: 332–345.

HAYS, H. 1972. Polyandry in the Spotted Sandpiper. Living Bird 11: 43–57.

HILDÉN, O. 1975. Breeding system of Temminck's Stint *Calidris temmincki*. Ornis Fennica 52: 117-146.

HOLLAND, P. K., J. E. ROBSON, & D. W. YALDEN. 1982. The breeding biology of the Common Sandpiper *Actitis hypoleucos* in the Peak District. Bird Study 29: 99-110.

JENNI, D. A. 1974. Evolution of polyandry in birds. Am. Zool. 14: 129-144.

———, & G. COLLIER. 1972. Polyandry in the American Jacana (*Jacana spinosa*). Auk 89: 743-765.

LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen.

LANK, D. B., L, W. ORING, & S. J. MAXSON. 1985. Mate and nutrient limitation of egg-laying in a polyandrous shorebird. Ecology 66: 1513-1524.

MAYNARD SMITH, J., & M. G. RIDPATH. 1972. Wife sharing in the Tasmanian Native Hen, *Tribonyx mortierii*: a case of kin selection? Am. Nat. 106: 447-452.

MURRAY, B. G., JR. 1979. Population dynamics: alternative models. New York, Academic Press.

———. 1984. A demographic theory on the evolution of mating systems as exemplified by birds. Pp. 71-140 *in* Evolutionary biology (M. Hecht, B. Wallace and G. Prance, Eds.). New York, Plenum.

———. 1985a. The influence of demography on the evolution of monogamy. Pp. 100-107 *in* Avian monogamy (P. A. Gowaty and D. W. Mock, Eds.). Ornithol. Monogr. 37. Washington, D.C., Am. Ornithol. Union.

———. 1985b. Evolution of clutch size in tropical species of birds. Pp. 505-519 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. 36. Washington, D.C., Am. Ornithol. Union.

———. 1990. Population dynamics, genetic change, and the measurement of fitness. Oikos 59: 189-199.

———. 1991. Sir Isaac Newton and the evolution of clutch size in birds: a defense of the hypothetico-deductive method in ecology and evolutionary biology. Pp. 143-180 *in* Beyond belief: randomness, prediction, and explanation in science (J. L. Casti and A. Karlqvist, Eds.). Boca Raton, Florida, CRC Press.

———, & V. NOLAN JR. 1989. The evolution of clutch size. I. An equation for predicting clutch size. Evolution 43: 1699-1705.

———, J. W. FITZPATRICK, & G. E. WOOLFENDEN. 1989. The evolution of clutch size. II. A test of the Murray-Nolan equation. Evolution 43: 1706-1711.

NEWTON, I. (Ed.) 1989. Lifetime reproduction in birds. New York, Academic Press.

NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithol. Monogr. 26. Washington, D.C., Am. Ornithol. Union.

ORING, L. W. 1982. Avian mating systems. Pp. 1-92 *in* Avian biology, vol. 6 (D. S. Farner, J. R. King and K. C. Parkes, Eds.). New York, Academic Press.

———. 1986. Avian polyandry. Pp. 309-352 *in* Current Ornithology, vol. 3 (R. F. Johnston, Ed.). New York, Plenum.

———, & M. L. KNUDSON. 1972. Monogamy and polyandry in the Spotted Sandpiper. Living Bird 11: 59-73.

———, D. B. LANK, & S. J. MAXSON. 1983. Population studies of the polyandrous Spotted Sandpiper. Auk 100: 272-285.

PITELKA, F. A., R. T. HOLMES, & S. F. MACLEAN JR. 1974. Ecology and evolution of social organization in arctic sandpipers. Am. Zool. 14: 185-204.

SUMMERS-SMITH, J. D. 1988. The sparrows: a study of the genus *Passer*: Calton, England, Poyser.

WOOLFENDEN, G. E., & J. W. FITZPATRICK. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Princeton, Princeton Univ. Press.