Breeding system of Temminck's Stint *Calidris temminckii*

Olavi Hildén

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An isolated, colour-ringed population was studied for 10 years on the west coast of Finland. The breeding strategy is a double-clutch system associated with successive bigamy. Every female pairs in rapid succession with two males on different territories and lays one clutch on each. Every male also pairs successively on the same territory with two females and fertilizes one clutch of each. The first clutch is incubated by the male, the second by the female, and both take sole responsibility for their brood. Exceptions to the normal schedule occur fairly often, chiefly due to the polygynous tendency in males. They court every female that enters their territory, so two females occasionally lay their first clutches on the same territory. Replacement nests are very rare. Roughly one-third of the females shift their breeding grounds from year to year and also lay their two clutches in different areas during a single breeding season.

Besides in Temminck's Stint, variations of the rapid multi-clutch system have been revealed so far in seven other wader species *(Calidris alba, Charadrius montanus, Tringa macularia, Phalaropus lobatus, Eudromias morinellus, Rostratula benghalensis, Jacana americana),* in some of them as a regular strategy, in others occasionally. Evolution of the multi-clutch system from the ancestral monogamous system with its persistent pair bonds and shared parental responsibilities could have proceeded along two main lines: either the female lays one clutch attended by a male and a second which she incubates herself (as in Temminck's Stint), or she lays clutches that are incubated by more than one male (polyandry). The selective advantage of multiple clutches is the potentially increased number of offspring, but this is counteracted by the loosening of pair bonds, increased losses of eggs and young because only one bird can carry out parental duties, and increased demands on the female by laying more than one clutch. The availability of food during the laying period is thought to be the decisive factor: only those species or populations living in very productive habitats with abundant food supplies have been able to evolve the rapid multi-clutch system. High predation rates have intensified selection for production of multiple clutches. On the other hand, the strong pair bond may have prevented the evolution of multi-clutch system in species having potentially good qualifications for this breeding strategy.

There is no general adaptation towards reduced clutch size in species exhibiting rapid multi-clutch systems, nor do they show any clear trend towards prolonged laying intervals between clutches, or delayed sexual maturity. In four species the eggs are slightly, and in two greatly reduced in size, whereas in two species there is no reduction. A characteristic adaptation in Temminck's Stint is the delay of the male's incubation for several days, during which he continues to display and is able to fertilize a second clutch.

Introduction

Recently the biology of several wader species have received intensive study. Some 10—15 years ago, information about wader breeding biology and behaviour was derived chiefly from scattered observations made during faunistic surveys, but now comprehensive population studies have been published on many species. For the sandpipers (genus *Calidris*), these include the Pectoral Sandpiper *Calidris melanotos* (Pitelka 1959, Holmes 1966, Norton 1972), Curlew Sandpiper *C. ferruginea* (Portenko 1959, Holmes & Pitelka 1964), Baird's Sandpiper *C. bairdii* (Drury 1961, Norton 1972), White-rumped Sandpiper *C. fuscicollis* (Drury 1961, Parmelee, Greiner & Graul 1968), Western Sandpiper *C. mauri* (Brown 1962, Holmes 1971a, 1972, 1973), Red-backed Sandpiper or Dunlin *C. alpina* (Heldt 1966, Holmes 1966, 1970, 1971b, Soikkeli 1967, 1970a, 1970b, Norton 1972), Purple Sandpiper *C. maritima* (Bengtson 1970), Sanderling *C. alba* (Parmelee 1970, Parmelee & Payne 1973), Semipalmated Sandpiper *C. pusilla* (Norton 1972), Stilt Sandpiper *C. himantopus* (Jehl 1973), and Knot *C. canutus* (Nettleship 1974).

Special attention has been paid in recent years to the mating systems and their evolution in waders, i.e. the pair relationship and participation of mates in parental duties (Hogan-Warburg 1966, Lack 1968, Hays 1972, Jenni & Collier 1972, Oring & Knudson 1972, Graul 1973, Jenni 1974, Pitelka, Holmes & MacLean 1974). A wide variety of different patterns or strategies has been found, some species being monogamous, ohers polyandrous, polygynous or promiscuous. A special breeding system is shown by some waders in which females lay more than one clutch in rapid succession. So far, the existence of such a system has been demonstrated convincingly in Temminck's Stint *Calidris temminckii* (Hildén 1965, Kochanow 1973), Sanderling (Parmelee & Payne 1973), Spotted Sandpiper *Tringa macularia* (Hays 1972, Oring & Knudson 1972), Mountain Plover *Charadrius montanus* (Graul 1973), Painted Snipe *Rostratula benghalensis* (Lowe 1963, Ali & Ripley 1969, Jackson 1970), and American Jacana *Jacana spinosa* (Jenni & Collier 1972, Jenni 1974); to some extent it is known to occur also in the Red-necked Phalarope *Phalaropus lobatus* (Hildén & Vuolanto 1972, Raner 1972) and Dotterel *Eudromias morinellus* (Pulliainen 1971, Nethersole-Thompson 1973). However, there are considerable differences between these species as to the mating system and the participation of both sexes in parental duties. This diversity raises a number of fascinating problems: how have all these systems evolved, what is the survival value of the different adaptations, and why has evolution diverged in so many directions even in closely related species?

In 1963, I started a population study of Temminck's Stints on the west coast of Finland at the southern border of the species' range. The study continued for ten breeding seasons, up to and including 1972. Until now, only two preliminary reports (Hildén 1965, 1972) and an analysis of the variation in egg dimensions (Väisänen et al. 1972) have been published. This paper presents my data on the breeding system of the species. Information on breeding biology, behaviour, dispersion pattern, site tenacity and population dynamics has been given only when appropriate; these topics will be reported in detail later.

The distribution of Temminck's Stint extends throughout the tundra zone of Eurasia, from Scandinavia in the west to Bering's Sound in the east. In Fenno-

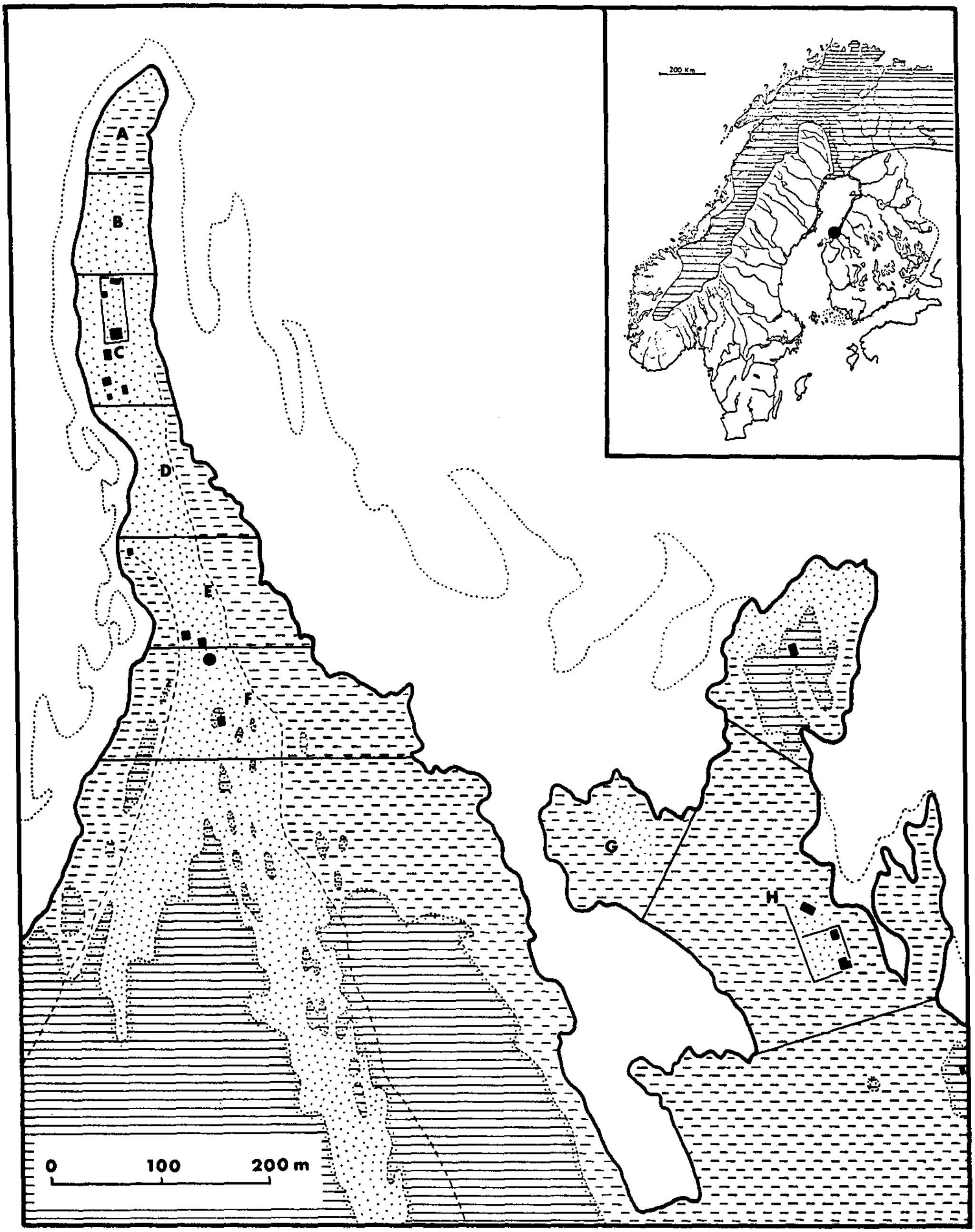


FIG. 1. The eight study areas (A—H) on Harrbåda (the western cape) and Rummelö (the eastern cape). Solid lines = woods, broken lines = meadows, dotted areas = sand with sparse vegetation. Shore areas within the dotted line are mudflats exposed during low water. The breeding range of Temminck's Stint in NW Europe according to HAFTORN (1971) and the geographical location of the study area are shown on the inset.

TABLE 1. Numbers of Temminck's Stint nests found during egg-laying or after clutch completion at Kokkola in 1963—72.

Year	Found incompleted 1 egg	2 eggs	3 eggs	Total	Found completed	Total
1963	1	3	3	7	17	24
1964	9	2	1	12	13	25
1965	8	1	1	10	13	23
1966	15	4	2	21	10	31
1967	12	2	5	19	13	32
1968	8	3	1	12	16	28
1969	1	0	2	3	16	19
1970	2	2	0	4	10	14
1971	8	0	0	8	6	14
1972	3	0	0	3	9	12
Total	67	17	15	99	123	222
%	30.2	7.7	6.8	44.6	55.4	100

scandia, the species breeds on the coast of the Gulf of Bothnia, almost isolated from the main breeding areas farther north and east (Fig. 1). Although Temminck's Stint is one of the commonest and most widely distributed Eurasian sandpipers, with a total population estimated at more than 10 million individuals (USPENSKI 1969), its biology was poorly known at the time I started my study. In addition to the general information in handbooks and faunistic surveys, only two reports dealing specifically with the breeding biology of the species were available (HAVILAND 1916, SOUTHERN & LEWIS 1938). Quite recently a Russian study on the ecology of Temminck's Stint on the Murman Coast was published (KOCHANOW 1973).

Study area and methods

1. *Study area.* The field studies were carried out at Kokkola (63°52'N, 23°05'E). The study area consists of the narrow cape of Harrbåda, about 600 m long and 50 to 200 m wide, and the adjacent meadows of Rummelö on the opposite side of a shallow bay (Fig. 1). To facilitate description of the field work, Harrbåda was divided into six and Rummelö into two part areas using conspicuous land marks (buildings, bushes etc.). These areas are shown in Fig. 1.

The Harrbåda cape is of sand, covered with a sparse vegetation of grasses, herbs and moss; the dominant plants include *Elymus arenarius, Deschampsia flexuosa, Chrysanthemum vulgare, Honkenya peploides* and *Silene inflata.* In many places the sand is bare, and there are several pits in the ridge, particularly favoured as nesting sites by Temminck's Stints. More luxuriant meadows are found on the eastern side of the cape. Except for scattered willow bushes and some small planted alders and rowans, trees are absent. The shores are lined by a thick growth of *Phalaris arundinacea,* with belts or patches of *Scirpus tabernaemontanii, Eleocharis uniglumis* and *Phragmites communis* extending into the water in places. The whole shore vegetation has expanded and grown more luxuriant in recent years due to pollution of the waters. When the water-level is low, the cape is surrounded by extensive mudflats.

There are some summer cottages with surrounding outhouses, fences, poles etc. on the cape. These are of great significance for Temminck's Stints, first because males use all kinds of elevated sites when giving their territorial songs and second because the even, sparsely vegetated house yards conform well to the species' habitat requirements. Similarly, large boulders lying scattered on the cape are important as song posts of males.

The Rummelö area is flat meadow with several shallow ponds and scattered boulders. Temminck's Stints are attracted only to those parts of the meadow where the vegetation is very low or replaced by bare sand; here also the yards of summer cottages are particularly favoured.

In addition to Temminck's Stints, several other wader species inhabit the study area: the Ringed

Plover *Charadrius hiaticula,* Little Ringed Plover *Ch. dubius* and Oystercatcher *Haematopus ostralegus* favour the sandy parts, the Ruff *Philomachus pugnax,* Redshank *Tringa totanus,* Dunlin *Calidris alpina schinzii* and Lapwing *Vanellus vanellus* occur in the meadow areas. Altogether, 13 wader species have been observed breeding in the area (Casén 1960).

Kokkola is the southernmost permanent breeding locality of Temminck's Stint in Finland. During my ten years of study, the population increased slowly at first from about 27 adults present in 1963 to 33—36 in 1966—69 but then declined rather abruptly to only 15 birds in 1972. In addition, 1—2 pairs have nested almost annually in the nearby control area of Morsiussaari, located 2.5 km east of Harrbåda. The population at Kokkola is very isolated, the nearest breeding grounds being some 50 km to the north, in the delta of River Kalajoki. This latter area, inhabited by some 15—20 pairs, has been checked carefully only in 1971—72 to search for birds ringed at Kokkola. North of Kalajoki, Temminck's Stints are found breeding in many places along the coast.

2. *Methods.* Field work commenced each year in late May, soon after arrival of the first Temminck's Stints. Work was continued until late July when all young were fledged. In 1963—65, I carried out most of the field work myself but in later years I usually stayed at Kokkola only during the early phase of the breeding season (to 6—12 June) and thereafter left the checking of nests and ringing of young to one or two assistants. In 1969 and 1970, all field work was conducted by my assistant Mr. Harri Hongell.

Temminck's Stint is in many respects a good species for a population study. First, it lives in open terrain, which makes the observation and recording of colour ringed birds relatively easy. Second, it occurs at high densities in suitable habitats. Third, Temminck's Stints are rather tame. Usually one can watch birds without disturbing them from 15—20 m, and some fearless parents may tend their young almost at the observer's feet. Fourth, the species very rarely deserts its nest due to human interference, even when the female is captured during laying.

Most nests are found in the same areas year after year. These areas were searched before the onset of egg-laying to find nest scrapes of males, which were then checked daily. This allowed observations to start right after laying of the first egg. Table 1 shows that almost half the nests were found during egg-laying and nearly one third at the 1-egg stage.

Adult birds were marked with both coloured and numbered rings. They were captured at the nest by a simple automatic trap. In total, 85 adult birds (31 males, 51 females, 3 of unknown sex) were colour-ringed in the course of the study. This represents about 80 % of the total population of the area during the study. The birds were numbered according to the trapping order, and these numbers are used as individual symbols in this paper (M = male, F = female). Of the few birds without colour-rings that were present annually in the population (mostly non-breeding individuals or birds which had lost their nests), about half had been marked as nestlings with aluminium rings only. In most cases, numbers on the rings could be read by a 40 × telescope. A total of 323 young were ringed in the course of this study.

As will be shown later, most females lay two clutches in the area and leave the first to be incubated by the male. To solve which females laid the clutches subsequently incubated by males, it was necessary to capture birds when laying eggs. This required checking the trap at frequent intervals. Attempts to capture egg-laying females were made at 56 nests, 46 (82 %) of which were successful; 29 birds laid an egg while still in the trap and 15 later, usually soon after being released, and only 2 females deserted their nests following trapping. Ten attempts to trap egg-laying females failed mainly because the trap had been released either by wind or the male before the female had come to the nest. Sometimes it was possible to identify the female which had laid a certain clutch by the specific form, colour and/or measurements of the eggs.

3. *Separation of the sexes.* The sexes of Temminck's Stint are very much alike and not easy to distinguish in the field. On average, the female is slightly larger and has more brownish pattern on her back than the male. Usually these

Table 2. Weights and wing and bill lengths of Temminck's Stints at Kokkola in 1963—72. If the same individual was weighed more than once, a mean weight has been used.

		Males				Females			
		Extremes	Mean	±S.D.	n	Extremes	Mean	±S.D.	n
Weight	(g)	22.0— 26.0	24.3	±1.17	31	26.0— 29.5	27.8	±1.19	28
Wing	(mm)	90.0—102.0	97.4	±0.67	20	93.0—105.0	98.0	±0.48	27
Bill	(mm)	15.1— 18.0	16.7	±0.19	16	16.0— 18.6	17.1	±0.17	17

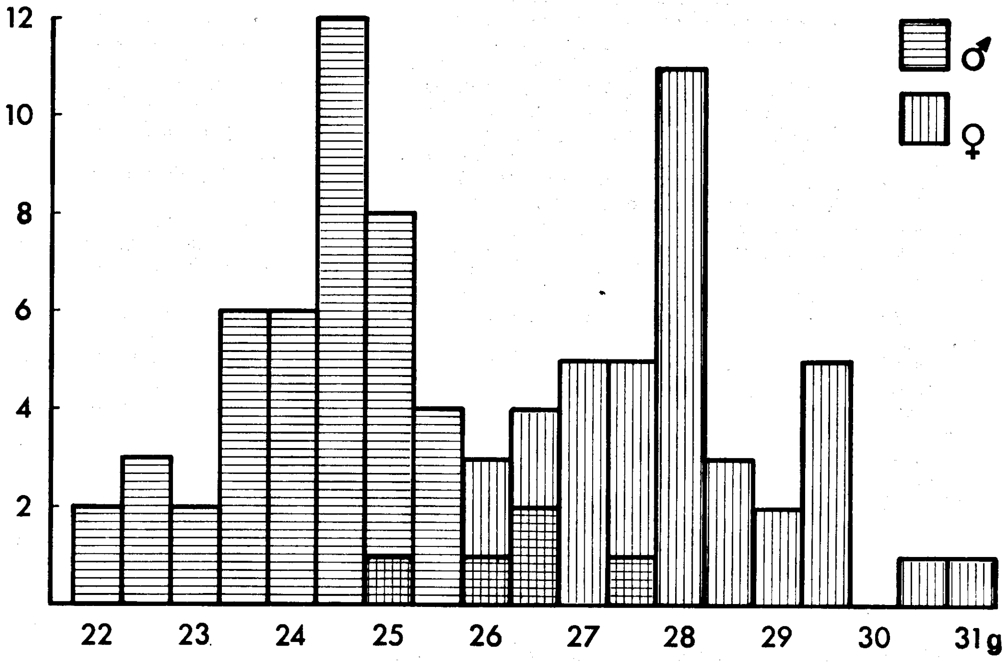


FIG. 2. Frequency distribution of weights of male (horizontal hatching) and female (vertical hatching) Temminck's Stints at Kokkola. Repeat weighings of the same individuals are included as separate observations.

small differences in appearance are observable when the birds are seen together but do not enable certain sexing of solitary birds. In many cases, however, it is possible to tell the sexes apart by differences in behaviour (voice, postures, movements, etc.). Gravid females about to lay eggs are easy to recognize by their thick, hanging cloacal region.

In the hand, most Temminck's Stint can be sexed by weight: birds weighing less than 26 g are usually males, those weighing more than 26 g are females (Table 2). The values given in the table are means for each bird (18 were weighed 2 to 5 times). The weight of an individual bird can vary considerably: M 6, for instance, weighed 24.5 g on 6 June 1963, 27.5 g on 26 June 1963 and 22.0 g on 4 June 1965 thus showing both extreme values for males! Fig. 2 presents all weights of Temminck's Stints taken at Kokkola showing the slight overlap of the sexes around 26 g. Females trapped at the nest during egg-laying are not included; they weigh up to 38 g. In wing and bill length there are no significant differences between the sexes (Table 2).

Breeding system

1. Summary of the breeding schedule. The breeding system of Temminck's Stint is peculiar in many respects. Each female normally lays two clutches, the first one subsequently incubated by the male, the second one by herself. She first pairs with one male and lays a clutch on his territory. As soon as this is completed, she leaves her mate, seeks a new male intent on pairing and, 2—4 days later, lays a second clutch on this new territory. Usually these nests are situated more than 100 m apart. The female commences steady incubation immediately after completion of the second clutch, whereas the male delays the onset of incubation for several days. During this period he still courts females appearing on his territory and often mates with a new bird. Usually this is a female which has already been paired with one male and is seeking a new mate for her second clutch. Consequently, most males have two clutches laid on their territories by different females. Each male and female takes sole responsibility for its nest and brood.

Fig. 3 illustrates a simplified case in which the population comprises only two males and two females. In this case, both males pair in turn with both females and thereby exchange their mates. The situation is much more complicated in larger populations (see p. 126).

2. *Pair bonds.* The pair bonds in Temminck's Stint are complex compared to those in most other waders. During the first few years of my study I was unable to get a clear picture of the mating system. Most cases suggested successive bigamy connected with the double brood system described above. In both matings the pair bond lasts only about one week, i.e. as long as is needed for the formation and laying of one clutch of eggs. It is also rather loose: the male and the female are seen more often separately than together. Observations on colour-ringed birds indicated, however, persistent pair bonds during this short period, since most pairs seen on successive days when feeding, courting or copulating were formed by the same individuals. Some case histories:

M 26 and F 37/1966: On 26 May the pair was feeding sometimes together, sometimes separately, and copulated on the territory of the male. On 30 May a copulation; on 31 May a failed copulation, later both birds visited in turn the same nest scrape where the first egg was found. On 1 and 2 June they were feeding together. Later the male started to incubate the completed clutch.

M 51 and F 47/1967: On 25 May the pair was seen together steadily, and a failed copulation was recorded. On 28 May they copulated, on 30 May the female was trapped on the nest when laying her third egg. Later the male incubated this clutch.

M 52 and F 48/1967: On 26 May three copulation attempts, on 29 May a successful copulation was observed. On 1 June the female was captured on the nest when laying her third egg. Later the male started to incubate this clutch.

Besides these observations on definite pairs, I also recorded cases indicating simultaneous polygyny, polyandry or

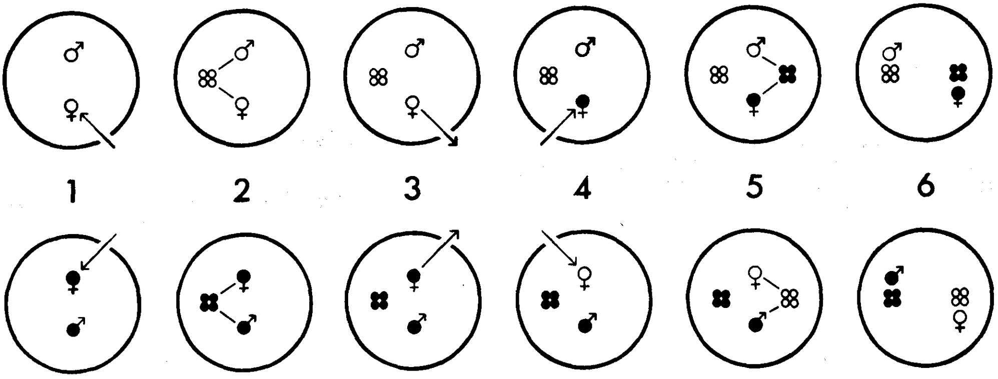


FIG. 3. Schematic representation of the breeding system of Temminck's Stint in a population comprising only two males and two females. 1—3: each female enters the territory (circle) of one male, pairs with him, lays a clutch and then leaves the territory; 4—5: each female seeks a new male, pairs with him and lays a second clutch; 6: the males start to incubate the first and the females the second clutches.

promiscuous mating systems. On several occasions one male was seen courting two females, either at the same time or at short intervals. The following examples may illustrate such cases:

M 9/1965: On 26 May within an hour, the male was seen courting F 11 and an unringed bird, both just as exitedly. On 3 and 4 June he was feeding together with F 11, later he incubated the clutch laid by this female.

M 30/1965: On 4 June the male followed F 22 and made repeated copulation attempts, but the female rejected him. A little while later on the same day he copulated with F 31, the clutch of which he then started to incubate.

M 51/1968: On 30 May the male at first fed closely together with an unringed female, then about six hours later he copulated with F 12. On 31 May he copulated successively with F 68 and the unringed bird, in the evening he was seen courting simultaneously F 12 and F 68, which fought together like two males.

In addition, I recorded some occasions on which one female was courted by two males, either simultaneously or on successive days. Three examples:

F 25/1964: On 13 June when the female was laying her second egg, M 15 was trilling exitedly all the time close to the nest, sometimes "hanging" in the air above it, sometimes running around it. Also M 24 tried repeatedly to come to the nest but was chased away by M 15 (several fights); in the evening M 24 was captured in a trap placed on the nest. Later the clutch was incubated by F 25 (her third clutch, cf. p. 128).

F 22/1965: On 4 June M 30 tried to copulate repeatedly with this female but she rejected him; after half an hour she copulated on the same spot with M 1. This male started to incubate the first clutch of F 22.

F 23/1965: On 10 June the female was seen together with M 26 who courted her lively and made copulation attempts but was rejected; at times small conflicts occurred between the birds. On 11 June she was courted eagerly by M 6 on the adjacent territory; in the evening, as well as on 13 June, both birds were seen close together. The female laid her second clutch on this territory (first egg on 13 June) and incubated it herself.

As puzzling as the mating system of Temminck's Stint may appear on the basis of individual observations, my overall notes reveal a fairly clear pattern to the pair-relationship. Each male occupies a territory and announces his presence through display, which serves to repel other males and attract females. Once a female appears on the territory, the male courts her, performs nest-scraping and tries to copulate. Since the females are sedentary, each one staying most of the time before and during egg-laying along the same small length of shore, the male normally pairs with only one female at a time. This result is also promoted by the intolerance of females towards each other (see the aggressive combats between F 12 and F 68, mentioned above), which tends to space them over the whole area.

However, if another female, e.g. a bird late to arrive, enters the territory, the male courts even her in the same way, and on several occasions one male has been seen copulating or trying to copulate with 2—3 females on the same day or on successive days. Similarly, a female keeping near the boundary between two territories attracts both males, which compete with each other for the opportunity to mate with her. Accordingly, the males are potentially polygynous, even though in practice most males pair with only one female at a time. Owing to this polygynous tendency in males, every female appearing on the territory attracts them, regardless of her attitude; also totally passive or even aggressively defending females are courted exitedly.

A good example is provided by the behaviour of an one-year-old male, which appeared in the area on 11 June 1965 and remained unpaired. At this advanced date two females, F 11 and F 12, were already incubating their clutches in the very area that was occupied as a territory by this late arriving male. As soon as either of these females left her nest to feed, she was followed by the courting male who performed display flight above her, circled exitedly trilling around her and tried to invite her to a nest scrape. By that date the females had lost their sexual potency and showed no interest in the courtship of the male.

The inclination of females to simultaneous polyandry, if it exists at all, is clearly weaker than that of the males. Some instances of one female with two courting males have been recorded, it is true, but the formation of these trios is attributable to simultaneous mating attempts by two neighbouring males, and not to any active seeking for two males by the female. On the contrary, in all cases I recorded, the female has rejected the copulation attempts of one male. There is also no evidence that a female copulated with two males during the laying of one set of eggs. Not until the female has completed her first clutch does she leave her mate and pair with a new one.

3. *Mate-faithfulness.* Theoretically, a female laying two clutches during one breeding season, either may form a persistent pair bond with one male, or may pair successively with two different males. In the former case both clutches would be located close to each other, within the territory of the same male; in the latter case they would lie farther apart.

As stated before, the latter alternative represents the normal case in Temminck's Stint. Each year I have recorded in the field cases in which an individually-known female at first associated with one male and then, after completing the first clutch, formed pair bonds with another. That this is the normal system is also documented by the locations of the first and second nests of the same females, which usually lie far apart. The tabulation below shows the distances between the successive clutches in all 40 cases recorded (range 4 to 950 m, average 247 m):

Distances (m)	N	%
0— 50	7	17.5
51—100	6	15.0
101—200	11	27.5
201—300	7	17.5
301—500	2	5.0
501—700	3	7.5
701—900	2	5.0
901<	2	5.0

Only in 13 cases were the first and second nest less than 100 m apart, but even then the female was known to have paired with two different males in at least 6 cases. On the remaining 7 occasions mate-faithfulness during both clutches could not be proven definitely. The most probable instance refers to F 37 in 1966, which laid her both clutches only 4 m apart on the territory of M 26. However, the first egg of the second clutch was laid in the morning of 11 June, by which date M 26 was already incubating the first clutch steadily. So it is possible that the second set of eggs of F 37 was fertilized by one of the neighbouring males, which in this part of the area were concentrated close to each other. To conclude, if mate-faithfulness during the same breeding season does occur in Temminck's Stint, it is exceptional.

The first pair bond is broken immediately after completion of the first clutch. Already on the same or the following day I have recorded females associating with a new male far from the first nest site. Two examples:

F 23/1965: The fourth egg of the first clutch, situated in area H, was laid on 9 June at 09.30 hrs. On 10 June at the same time the female was found in area C, about 800 m from her first nest site, engaged in courtship display with the territory holding M 26. Next morning she was seen in courtship activities with M 6 about 70 m from the above place; the second clutch was laid on the territory of this male.

F 79/1971: The first clutch was situated in area H and completed on 6 June at about 11.00 hrs. At 17.30 hrs the same day the female was found in area A, almost 1 km from the first nest site, together with M 73 that was courting her exitedly. Later the second clutch was found on the territory of this male.

All the facts described above show convincingly that PARMELEE & PAYNE (1973) have totally misunderstood the mating system of Temminck's Stint when they discuss my earlier paper (HILDÉN 1965). According to them, "the male consorts with the female for several days after the first clutch is laid, apparently competing with other males for the opportunity to mate with her and to fertilise a second set of eggs". Such instances have never been observed, nor did I suggest this in my paper. The authors also state incorrectly that "rarely are both male and female Temminck's Stints taken with a single brood". Without a single exeption there was always only one incubating bird on each nest, either a male or a female.

I also doubt the validity of KOCHANOW's (1973) conclusion, that on the Murman Coast male and female Temminck's Stint maintain their pair bonds throughout the breeding season and that both clutches are laid within the same territory. According to him, this is indicated by the location of nests in pairs 5—45 m apart, with 30—200 m between adjacent pairs of nest. But these facts alone do not allow such a conclusion; the same distribution of nests also follows if each male pairs successively with two females on his territory. As the persistence of pair bonds was not shown directly by means of ringed birds, possible geographical differences in the mating behaviour remain unproven.

Those calidridine species which have strong monogamous pair bonds, like the Dunlin (SOIKKELI 1967, 1970a) and the Western Sandpiper (HOLMES 1971a), have been found to show a high degree of mate-faithfulness from one year to the next. In Temminck's Stint, with short and loose pair bonds formed each year with two successive mates, one would hardly expect high mate fidelity. In 5 cases out of 25 was the first mate of a certain individual the same in two consecutive seasons. However, since only 15 of the previous mates had returned, these figures mean that of birds still alive about every third rejoined its mate of the previous year. Although mate-faithfulness is much weaker than in the Dunlin and Western Sandpiper, the frequency of remating nevertheless is significantly higher than would be expected if matings were random (see Appendix). This tendency to remating is without doubt attributable to the strong site tenacity of the species: the males almost invariably occupy the same territories year after year, and also half the females return to the same part of the area (HILDÉN, unpubl.). For this reason, the chances for a certain individual to rejoin its former mate, if still alive, are considerable. For second pairing, my few observations indicate that mate-faithfulness is probably of the same order as that during the first pairing.

4. *Other breeding schedules.* Exceptions to the normal mating system of Temminck's Stint occur fairly often. Such special cases include the following.

Males with two females, both laying their first clutch. As mentioned earlier (p. 124), on several occasions one male has been seen courting two females, either at the same time or at short intervals. If both females are going to lay their first clutch, the male will have two clutches to take care of. Six such instances have been revealed in the course of the study, concerning four different males.

M 9/1964: The nests, both with 4 eggs, were situated 25 m apart. The first nest was found on 14, the second one on 15 June, and M 9 was incubating on both when found! On later controls, he was always incubating on the first nest and thus had deserted the other one. The young hatched on 6 July.

M 6: This male, a real "Don Juan", attracted in three successive years two females to lay their first clutch on his territory. In 1965, one clutch was laid between 31 May and 3 June. The male was seen to visit this nest on 4 and 8 June, yet he did not commence a steady incubation and soon abandoned the nest. Instead he was found on 14 June incubating another nest, situated 39 m from the first one, and continued the incubation until the nest was destroyed on 21 June.

In 1966, the first nest (with F 36) was completed on 27 May, and the second one (with an unringed female), 44 m apart, was laid on 3—7 June. The male was not recorded one single time on the first nest, but on 9 June he started to incubate the second one. The young hatched on 29 June.

In 1967, the first nest (with F 43) was completed on 1 June, the second one was found as completed on 12 June from 20 m away. Eggs in the first nest were cold at each check on 2—6 June, but on 7 June M 6 was flushed twice from the nest; the following day the nest was destroyed. On the second nest, M 6 was already incubating when found; the young hatched on 3—4 July.

M 41/1967: Both clutches (with F 49 and F 50) were laid between 31 May and 3 June and were situated about 120 m apart. On 7 June the male started to incubate one of the clutches; the following day this nest was destroyed but the bird continued incubation on the other nest. The young hatched on 29 June.

M 51/1968: The male courted simultaneously F 12 and F 68 (see p. 124). The latter female laid her clutch between 31 May and 4 June, but the nest of F 12 was not found until completed on 8 June. The distance between both nests was 33 m. On 9 June the male started to incubate the clutch laid by F 68 and left the other one unattented.

These observations show that the male may at first try to incubate both clutches but soon desert one. In two cases, after the nest on which incubation had commenced was destroyed, the bird shifted to incubate the other one. Only in these cases was it advantageous for a male to have two first clutches on his territory, the other one as a "reserve nest"; otherwise, one of the clutches is always doomed to go to waste.

Three facts suggest that laying of two first clutches on the territory of one male occurs more frequently than the six cases recorded. First, males simultaneously courting two females have been recorded fairly often (cf. p. 124). Second, if a male is found incubating one nest, any unattended additional nest on his territory is very likely to be overlooked if not found during egg-laying. Third, in addition to the six definite double nests mentioned above, I found four completed clutches that remained unincubated, probably because they were "excess nests" of males.

Two females laying in the same nest cup. In 1968, two females (F 54 and F 57) paired simultaneously with the same male (M 30) and laid by turns in the same nest cup. The nest was completed on 6 June and consisted of 7 eggs. This was the first clutch of F 57 and the second one of F 54, which consequently started to incubate the shared nest. The incubating bird probably prevented F 57 from laying her last egg in the nest, for which reason she laid it in a new nest cup 38 m away. This last egg of the first clutch was also the first one of the second clutch: after an interval of three days, F 57 laid again in the same nest but laid only two additional eggs.

BOTTOMLEY & BOTTOMLEY (1973) have reported a similar case from Swedish Lapland: a Temminck's Stint nest containing 7 eggs, clearly laid by two females and incubated by one bird.

A male with no nest paired with a female going to lay her second clutch. At times there must be situations in which a male either has no clutch to incubate or has lost it before he pairs with a female about to lay her second clutch. The question is, which bird subsequently incubates the nest.

Unfortunately, my data are few because the male which has fertilized the second clutch often remains unknown. Of the few identified males only three have been known for certain to be without a first clutch at the date of the second pairing. In all these cases, the female started to incubate and the male was not once seen to share in incubation.

The most probable explanation is that the immediate start of incubation by the female at her second nest prevents the development of an incubation drive in the male. As mentioned before, the male normally delays the onset of incubation for some days, during which he continues to display. Evidently the gradual change from display to incubation behaviour is released by the uncovered clutch. If the female is sitting on the eggs most of the time, the male's incubation drive will be inhibited.

A female laying three successive clutches. Two instances have been recorded in which the same female laid three clutches in rapid succession. The first two she left to males and incubated the third one herself.

F 25/1964: The female completed her first clutch the night between 3 and 4 June. The first egg of her second clutch was laid on 6 June at 10.30 hrs and the fourth one in the evening of 9 June. Laying of the third clutch began on 12 June at 20.00 hrs, and the female commenced steady incubation immediately after clutch completion on 16 June. The second clutch remained unattended because the male (an unringed bird) disappeared soon after pairing.

F 12/1968: The first and second clutch were found as completed on 30 May and 8 June, respectively. Although the female was not trapped on the nest when laying, both clutches belonged certainly to F 12 judging from (1) the typical size and form of the eggs, (2) the staying of this female near both nest sites during egg-laying, and (3) her copulation with M 51, the owner of the territory on which the second clutch was laid. Also the third clutch was completed when found on 16 June, and it was incubated by the female. The second clutch was deserted because M 51 started to incubate a nearby clutch laid by another female (see p. 127).

Some triple clutches may have been overlooked, because confirmation requires either that the female is captured during egg-laying at the first two nests, or that the eggs are recognizable by their peculiar appearance. Anyway, triple clutches must be rare, since in nearly 40 cases it was proven that a certain female laid only two successive clutches.

The reasons which may force a female to lay three clutches in a season are not known. F 12, for example, laid two clutches in four consecutive seasons, from 1964 to 1967, but in 1968 she laid three. The reason cannot be a special behaviour of the second male, which would reveal that he will take care of the incubation and thus would give the female a chance to lay and additional third clutch, because in both cases I recorded the second clutch remained unattended.

Replacement nests. Because in Temminck's Stint each sex incubates its own clutch, males and females are in different places if a nest should fail. If a male loses his nest, his chance of getting a replacement clutch is dependent upon finding a new mate who has not yet laid her first clutch. A female, on the other hand, has only to find a male intent on pairing to fertilize the new set of eggs.

Hence, it must be more difficult for a male than a female to obtain a replacement clutch. By mid-June most females are incubating, and even if a male succeeds in attracting a new female into his territory, in most cases she is about to lay her second clutch. In the course of the study, 32 nests incubated by males were destroyed by 25 June, and only one of these males was found later incubating a substitute clutch. This was M 1 in 1964: his nest was robbed on 7 June, in the early stage of incubation, and the replacement nest was found on 24 June 14 m away from the first one. Thus, all the other males failed to get a new clutch, although display normally recommenced one or two days after the nest failure.

For a female which has lost her nest, finding a new mate is no problem if the season is not advanced. Until late June, there are always some males in the popu-

TABLE 3. Numbers of completed first, second and third Temminck's Stint clutches found at Kokkola in 1963—72. X-clutches refer to nests of unknown position in the laying sequence.

Year	First clutches	Second clutches	Third clutches	X-clutches
1963	13	9	0	1
1964	13	10	1	1
1965	14	6	1	0
1966	17	9	0	1
1967	16	13	1	0
1968	12	13	1	1
1969	10	7	0	2
1970	6	3	0	6
1971	7	6	0	0
1972	4	5	0	2
Total	112	81	4	13
%	53	38	2	7

lation who maintain their sexual activity (unpaired birds or males that have lost their nests). Nevertheless, of 13 nests incubated by females and destroyed by 25 June, only two were replaced:

F 23/1965: The second clutch was completed on 16 June and incubated steadily by the female until it was destroyed on 21 June. The bird was found incubating a new clutch on 30 June, at a distance of 190 m from the second nest.

F 12/1967: The female commenced incubation of the second clutch on 7 June, the day it was completed, but on the following day the nest was flooded by high water and deserted. On 15 June she was found incubating a replacement clutch 75 m away from the second nest.

In both these cases, the intervals between nest failure and the onset of laying a replacement clutch were at most 5 days. That other females failed to lay a substitute clutch might indicate lowered hormonal activity after laying of two clutches, i.e. they may be physiologically incapable of producing an additional third clutch.

5. *Do all females lay two clutches?* The total numbers of first and second clutches found are presented in Table 3. In addition to nests whose sequence was known from the females, all nests incubated by males were classified as first clutches, and those incubated by females as second clutches. Eight nests which remained unattended were also included as first clutches, because females always commence steady incubation of second clutches immediately after completion. The few nests in the category of "X-clutches" refer to cases in which (1) the nest was destroyed before the incubating bird was identified (8 cases), (2) the colour-rings of the incubating bird could not be determined (3 cases), or (3) the sex of the incubating bird remained obscure (2 cases).

If all females laid two clutches, one would expect about equal ratios of first and second clutches among the nests found. However, clearly more first than second clutches have been found (112 against 81); the difference is significant ($\chi^2 = 4.98$, $P < 0.05$). This cannot be due to any methodological error, e.g. that first clutches would be easier to find. Although first clutches are there to be found for a few days longer than second clutches (because of the delay in the start of their incubation), most nests are found either during egg-laying, by daily checks of the nest scrapes, or during incubation when the bird flies off the nest. On the other hand, first clutches are more often destroyed than second

TABLE 4. Numbers of "vagrant" and "faithful" female Temminck's Stints (see text) caught when laying their first clutch, and the percentages of those birds found incubating a second clutch in the same season.

	Controlled when laying the first clutch	Found in the same season incubating a second clutch
"Vagrant" females	13	4 = 31 %
"Faithful" females	40	34 = 85 %

ones (hatching successes of 52 % and 61 %, respectively), and nest failure may, of course, happen before the nest is found. This higher destruction rate of first clutches, and the fact that some "excess nests" of males probably have been overlooked (see p. 127), suggests that the difference between the numbers of first and second clutches laid should be slightly greater than recorded. As the second nests include 9 clutches of new birds, not present in the population at the date when first clutches were laid (see p. 131), the actual proportion of females laying only one clutch in the area is, according to the number of "missing" second nests, roughly one third.

About one third of the females do not return to the study area in the year after ringing but breed elsewhere (HILDÉN, unpubl.). This raises the possibility of a connection between these two groups. To test this, I have separated all 51 females colour-ringed in the course of the study into two categories: those which were not recovered in the area in the year after ringing (27), and those which bred in the area in at least two years (24). Of the former 27 "vagrant" females, 13 were trapped at their first nest during egg-laying. Later in the season, 4 of them were found when incubating their second clutches, while the remaining 9 where not recovered. The situation in the second group, females showing faithfulness to their breeding ground, is very different (Table 4).

It should be noted that the 27 females, classified as vagrant, included some potentially faithful birds, which did not return simply because they died during the winter. Since the mean annual mortality of adult females is c. 29 % (HILDÉN, unpubl.), their number can be estimated to be about nine. The same ratio of potentially faithful birds most probably is included also in the 13 females in Table 4. In that case, all four birds which laid a second clutch in the area actually belonged to faithful females. The conclusion is that vagrant females, which shift their breeding grounds from year to year, lay only one clutch in the area, while faithful females usually lay two. (The missing 15 % of second clutches of the 40 faithful females in Table 4 may have been destroyed before found.)

A further question is, do the vagrant females really lay only one clutch, or do they shift during a single breeding season to another area and incubate their second clutch there? This problem can be answered only indirectly. If, after laying their first clutch, they did not lay a second one, they probably either remained in the area for some time or migrated south immediately. In fact not one of the 9 birds involved (Table 4) was seen after completion of the first clutch, even though I searched for all females regularly. This suggests that vagrant females actually leave the area as soon as they have completed the clutch in early June. Southward migrating Temminck's Stints have not been recorded in Finland until one month later (Hildén 1961), so birds which disappeared must have moved to another area. Such behaviour would scarcely have been evolved without any biological value, so it must be assumed that they lay their second clutch in the new area; if they did not, they would produce only half the number of offspring of the double-nesting females. Any such genetic trait would soon be eliminated.

If the conclusions reached above are valid, then the emigration of vagrant females in June should be balanced by a corresponding immigration of other females that have laid their first clutches elsewhere. But it seems not to be so, since second clutches are clearly fewer in numbers than first ones (Table 3). The most probable explanation is that, in the southernmost parts of the breeding range, the movements of vagrant females between two breeding areas are directed mostly to the north, away from Kokkola. Such migration cannot be verified in the field, because it overlaps with the normal spring passage, which continues until about 10 June.

However, a few new females do arrive at Kokkola in June. This can be deduced from the high number of second clutches laid by the 27 females not recovered after the year of ringing. As many as 18 were found incubating a second clutch, 14 of them new, unringed birds (4 were ringed when laying their first clutch). Since 9 females were supposed to be faithful, half the incubating females were vagrant. As these lay their successive clutches in two different areas, they must have come to Kokkola from elsewhere. As further evidence, the eggs of some of these females had a size, form or colouring that did not fit any known first clutch in the area. Because nearly all second clutches were found and the incubating females captured, the 9 vagrant females detailed above must be very close to the actual number of late immigrants which appeared at Kokkola to lay their second clutches during the years of study. This amounts to not more than 20—25 % of the number of emigrants present in the population.

Proof of the suggestions could be made in two ways: (1) examination of the ovaries under a dissecting microscope, to show that all females lay two clutches (cf. Parmelee & Payne 1973), and (2) recovery of a female, ringed when laying her first clutch, in another area incubating her second clutch. The first method was not used since it would have involved killing several birds, which would have reduced the population under study. The second alternative would require checking vast areas along the coasts in order to find the missing females, which in practice is impossible. The nearest breeding area (in Kalajoki) was examined in 1971 and 1972, but without any success in this respect.

Discussion

1. *Multiple clutches in other wader species.* Graul (1973) has introduced the term "rapid multi-clutch system" for strategies in which females lay more than one clutch in rapid succession. Temminck's Stint was the first wader species in which such a mechanism was documented convincingly (Hildén 1965). Later similar systems have been revealed in other species, e.g. the Sanderling. Parmelee (1970) and Parmelee & Payne (1973) have shown that only a single bird, either male or female, incubates the eggs and attends the young. Although they were not able to prove by means of ringed birds that females may lay multiple clutches in rapid succession, an examination of the

ovaries of two females taken as the birds began incubation showed that they had laid two clutches of four eggs each within 8—10 days. This fits well with the observation that at both nests subsequently incubated by males, the females disappeared after laying the last egg and were not seen again. On a third nest, attended by a female, she started to incubate immediately after clutch completion.

The onset of incubation by the Sanderling male was different at the two nests under observation: one male commenced steady incubation almost immediately after clutch completion, the other delayed the start of incubation for nearly six days. During this period he could not be found on his territory, and the authors believed that the pair was attempting another nesting on another site. If this conclusion, based on a single observation, is valid, then the Sanderling differs from Temminck's Stint in which the male normally pairs with two females on the same territory. However, the maintenance of the pair bond during the laying of both clutches in the Sanderling is only a hypothesis; the male could have associated with a new female during his absence from the first nest site. So far the data are too few to determine the precise mating system of the Sanderling.

In other *Calidris* species this kind of breeding system has not been observed so far. It may occur in the Little Stint *C. minuta*, judging from an observation by KISTCHINSKI & FLINT (1973) of two nests, located about 7 m apart, one incubated by a male, the other by a female. The identical colouring of the eggs in both clutches suggested that they had been laid by the same bird. A shared nest containing 8 eggs, reported by REYNOLDS (1972), gives some indications of polygyny in the Little Stint (cf. p. 127).

The breeding system of the Mountain Plover has much in common with that of Temminck's Stint but shows also certain differences (GRAUL 1973). As in Temminck's Stint, the female lays two clutches in rapid succession, leaves the first one to the male and incubates the second herself. Another similarity is the looseness of pair bonds: the mates of a pair are commonly seen alone, and even when together they generally maintain an individual distance of 6 to 15 metres. Furthermore, Mountain Plover males seem to court each female that enters their territories, and the females may switch their mates prior to laying the second clutch, as in Temminck's Stint. The most important difference is that the female may remain with her original mate while she lays her second clutch, and even if remated with a new male she nevertheless places her second clutch within the original territory. The female Temminck's Stint, on the contrary, always forms successive pair bonds with two males and places her clutches on two territories some distance apart. The way in which males of the two species maintain their sexual activity after completion of the first clutch is also different. While Temminck's Stint males delay the onset of incubation for several days, Mountain Plover males commence incubation immediately; however, they do not attend the clutch steadily but continue to court and copulate with their mates or other females. Finally, the interval between the two clutches is 9 to 13 days in the Mountain Plover, against only 2 to 4 days in Temminck's Stint.

The Spotted Sandpiper also shows serial polygamy connected with multiple clutches, but the system differs in many respects from that found in Temminck's Stint (HAYS 1972, ORING & KNUDSON 1972). First, the roles of the sexes are reversed, the female being larger and more aggressive but less active in parental duties; therefore, she is polyandrous but each male is paired with only one female. Second, both mates may incubate on the same nest and take care of the same brood. There is much variability in pairing behaviour between females. Some nest with only one male and share the incubation with him, thus exhibiting a normal monogamous mating system. Others pair successively with two, three, or even four males and do not incubate until the final clutch; the previous males tend the eggs and young without the female's help.

In the Red-necked Phalarope, serial polyandry occur if excess males are present in the population (HILDÉN & VUOLANTO 1972, RANER 1972). The second clutch can be started only 5—6 days after completion of the first one. However, most females lay a single clutch. The reversal of sexual roles is very pronounced in phalaropes, the male incubating and taking care of the young alone.

The situation seems to be fairly similar in the Dotterel (PULLIAINEN 1970, 1971, NETHERSOLE-THOMPSON 1973). Most females lay only one clutch which they leave to the males, but some are polyandrous and lay a second clutch. In one well documented case described by PULLIAINEN (1971), laying of the second clutch commenced 4.7 days after completion of the first, and the distance between the two nests was 600 m. Contrary to the phalaropes, the female may share the incubation of the second clutch with the male (see also HILDÉN 1966).

In other species of the suborder Charadrii, multiple clutches have been demonstrated in the families Jacanidae (HOFFMANN 1949, JENNI & COLLIER 1972, JENNI 1974) and Rostratulidae (e.g. LOWE 1963, ALI & RIPLEY 1969, JACKSON 1970), in both connected with polyandrous social organization and concomitant reversal of sex roles. The best documented case refers to the American Jacana (JENNI & COLLIER 1972, JENNI 1974). This species inhabits small tropical ponds, and most females are polyandrous, simultaneously paired with 2 to 4 males. Eeach breeding male defends a small territory within the female's larger territory, and the female helps her mates repulse territorial intruders. The female may copulate with all her males on the same day and lays one clutch for each at intervals of 7 to 10 days, but does not share in incubation or care of the young. If a clutch is lost, a new one is laid within a few days. The basic difference between this system and those discussed above is the simultaneous mating of the female with two or more males; in all polyandrous species of the family Charadridae, the pair bonds are formed serially.

Outside the suborder Charadrii, polyandrous systems are very rare and have been demonstrated so far in only a few species of the orders Rheiformes, Tinamiformes, Gruiformes and (exceptionally) Passeriformes; however, in most of these species, the reports were based on indirect or circumstantial evidence (JENNI 1974). In addition, double-clutch production, not connected with polyandry, is known to occur in the order Galliformes: hens of the Red-legged Partridge *Alectoris rufa* may lay two clutches, one incubated by herself and the other by her mate (GOODWIN 1953, JENKINS 1957), just as in Temminck's Stint.

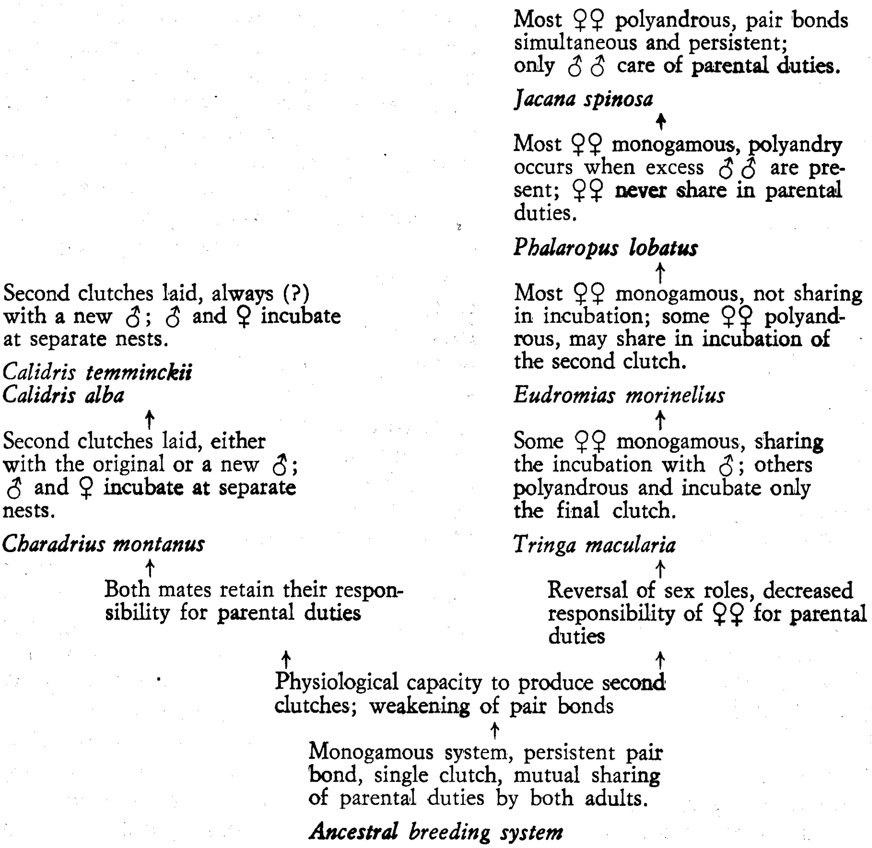
2. *Evolution of the rapid multi-clutch system.* The suborder Charadrii is characterized by tremendous variation in social systems. The monogamous system with persistent pair bonds and shared parental responsibility is the most common and probably the ancestral pattern of social organization in waders (cf. JENNI 1974, PITELKA, HOLMES & MACLEAN 1974). All other systems have

been evolved from this through natural selection, partly in response to highly variable environmental forces (availability of food, predation pressure, interspecific competition, diversity of habitat, climatic factors, etc.), but partly also in relation to other physiological or ecological adaptations of the species to its environment (feeding habits, breeding season, share of parental duties between the mates, timing of departure, sexual dimorphism, delayed sexual maturity, etc.). The present systems are compromises to these various selective forces, making the wide variety in strategies understandable. In the following section, I consider some important factors which probably have played a part in the evolution of the rapid multi-clutch system, an extreme form of breeding strategy.

Evolution of this system has proceeded along two main lines: either the female lays one clutch attended by a male and a second clutch which she incubates herself, or she lays clutches that are incubated by more than one male (polyandry). The Mountain Plover, Sanderling and Temminck's Stint represent the former evolutionary line, the Spotted Sandpiper, Red-necked Phalarope, Dotterel, Painted Snipe and American Jacana the latter one (Fig. 4). Two main questions arise: what are the advantages and disadvantages of the multi-clutch system, and why has evolution not led to the same strategy in other wader species?

Most waders lay a single clutch each season. A genetically determined capability of laying more clutches could be of definite selective value as he number of offspring can be increased. On the other hand, there are certain disadvantages compared with the original monogamous single-clutch system. First, incubation and care of the young by one parent instead of two may increase losses of eggs and young by exposing them more severely to weather and predators. Second, the rapid multi-clutch system is usually associated with loosening of pair bonds, which probably leads to decreased mate-faithfulness; this, in turn, may reduce the breeding success. Third, laying more than one clutch involves increased demands on the female. If these negative forces outweigh the selective advantage of multiple clutches, then the evolution of the multi-clutch system will be restrained. Let us examine closer these disadvantages.

NORTON (1972) has observed at Barrow, Alaska, that overall nest attendance after clutch completion amounted to 97.5 and 96.5 % in the Dunlin and Baird's Sandpiper, respectively, in which species both parents share in incubation, but to only 85.0 % in the Pectoral Sandpiper in which only the female tends the nest. The clutch is exposed to enemies and adverse weather when left unattended, so a lower rate of attendance may lead to a somewhat reduced hatching success and young viability. The average difference in breeding success between two-sex and single-sex incubating species is likely to be accentuated under severe conditions, especially in the arctic. According to NORTON (1972), time spent on the nest by the Pectoral Sandpiper decreases on colder days because of the increased energy costs of incubation and greater difficulty in securing insect prey. This can lead to severe egg chilling. In the Dunlin and Baird's Sandpiper, on the contrary, nest attendance increases at low temperatures. Also, two adults are probably better able to brood and protect their young than a single bird. In addition, if this single parent is killed during the incubation or brood period, the nest or young are doomed to destruction; but in the case of two attending adults, the death of either is not necessarily fatal as the other may manage the parental



Second clutches laid, always (?) with a new ♂; ♂ and ♀ incubate at separate nests.

Calidris temminckii
Calidris alba

Second clutches laid, either with the original or a new ♂; ♂ and ♀ incubate at separate nests.

Charadrius montanus

Both mates retain their responsibility for parental duties

Most ♀♀ polyandrous, pair bonds simultaneous and persistent; only ♂♂ care of parental duties.

Jacana spinosa

Most ♀♀ monogamous, polyandry occurs when excess ♂♂ are present; ♀♀ never share in parental duties.

Phalaropus lobatus

Most ♀♀ monogamous, not sharing in incubation; some ♀♀ polyandrous, may share in incubation of the second clutch.

Eudromias morinellus

Some ♀♀ monogamous, sharing the incubation with ♂; others polyandrous and incubate only the final clutch.

Tringa macularia

Reversal of sex roles, decreased responsibility of ♀♀ for parental duties

Physiological capacity to produce second clutches; weakening of pair bonds

Monogamous system, persistent pair bond, single clutch, mutual sharing of parental duties by both adults.

Ancestral breeding system

FIG. 4. Summary of the probable evolution of rapid multi-clutch systems in waders from the ancestral system, detailed at the bottom of the diagram. Evolution has proceeded along two main lines, but the breeding systems now exhibited by different species need not show phylogenetic relationships.

duties alone. However, the total effect of this factor can hardly be of decisive importance, because in several wader species, even in arctic regions, only one parent bird incubates and in many others either one of the mates abandons the brood soon after hatching.

The widespread occurrence of mate-faithfulness among birds shows that it must have some definite selective advantage. COULSON (1966, 1972) has been able to prove this convincingly in the Kittiwake *Rissa tridactyla*: birds which retain their mate nest earlier, lay larger clutches, have a better breeding success and produce more offspring, on average, than "divorced" birds. SOIKKELI (1967) has also emphasized the biological importance of mate-faithfulness in the Dunlin. Hence, a reduced mate fidelity may somewhat decrease the breeding success, but in no case can this disadvantage be so great that it could obstruct the evolution of the rapid multi-clutch system.

There remains the third disadvantage,

the increased demands on the female by laying more than one clutch, a heavy energetic expense during a short period. In Temminck's Stint, for instance, each female produces in about 10 days 8 eggs, the total weight of which corresponds to almost twice the bird's own weight! Whether or not a bird is capable of laying multiple clutches must depend decisively on the availability of food during a critical period. Consequently, only those species or local populations living in very productive habitats with abundant food supply have been able to evolve the rapid multi-clutch system. For species living in less productive habitats or specialized on a scarce food supply, production of two clutches in rapid succession would probably weaken the females so much that they would be unable to take care of the second clutch. The heavy expence of egg production could also lower the mean lifespan of females so that they would leave less offspring, in total, than females laying a single clutch.

What do we know about the food supply in species laying multiple clutches? In my study area at Kokkola, the main laying period of Temminck's Stints in the last days of May and early June coincides with the mass emergence of chironomids. At the same time of year the sea level is usually low and extensive mudflats are exposed along the shores. Hence, feeding conditions are very favourable for the laying females. Similarly, the timing of egg-laying in Red-necked Phalaropes at Norrskär, on the west coast of Finland, is adapted to the mass emergence of chironomids, which make second clutches possible (HILDÉN & VUOLANTO 1972). Hence, in these both species there is clear evidence of the role of high food availability in the production of two clutches.

The same idea applies to the Spotted Sandpiper. According to ORING & KNUDSON (1972), the evolution of multiple clutches in this species is a consequence of its colonization of the south temperate parts of North America. In these new areas, longer periods of high food supply have enabled the females to lay multiple clutches. Also the short interval, 5.3 days on average, between two successive clutches or between loss of the nest and initiation of the replacement clutch suggests availability of abundant food for laying females.

As regards the Mountain Plover and Sanderling, their multi-clutch systems seem to be adapted to the extreme fluctuations in food levels that occur in the habitats where they live (GRAUL 1973, PARMELEE & PAYNE 1973). The Mountain Plover inhabits the shortgrass prairie where sharp changes in insect food occur due to fluctuations in precipitation. The Sanderling lives in the high arctic where climatic conditions are often extremely variable from year to year with concomitant fluctuations in food supply. The authors suggest that females of these species adjust their reproductive efforts to food conditions by laying more than one clutch in good years but only one or perhaps none at all in poor years.

The same opportunistic strategy is likely to explain the cases of multiple clutches recorded in the Dotterel. I have studied this species in Finnish Lapland and I know how abrupt are the changes in food conditions on its breeding grounds: on warm, sunny days the insect abundance on fjell heaths is high, but during spells of cold weather, with strong winds and even heavy snowfalls, hardly any insects are to be found (cf. also RITTINGHAUS 1962, NETHERSOLE-THOMPSON 1973). Second clutches probably occur only under favourable food conditions.

Finally, as regards the American Jacana, its breeding habitat in small, shallow ponds with diverse and abundant aquatic flora represents a very rich tropical environment with high food density. Although the suitable space available for breeding territories is limited, and thus the food supply probably critical during the brood period, this does not restrict the availability of food for laying females because these also feed outside their territories on the surrounding lawns (JENNI & COLLIER 1972). In the protracted season of the tropics with constantly rich food resources, the females are able to aquire enough energy to produce multiple clutches in rapid succession. The same is likely to apply also to the Painted Snipe, living in tropical marshes or swamps with thick vegetation, shallow ponds and muddy patches, but very little is known about the biology of this species.

There are also more general observations that support the significance of high food supply in the evolution of the rapid multi-clutch system. First, for many species it is known that the frequency of renesting is affected by the food supply at the time of nest failure (e.g. SOUTHERN 1959, LACK 1966, SOIKKELI 1967). In arctic areas most waders fail to lay replacement clutches. According to HOLMES (1966), the Dunlin is the only wader species at Barrow, Alaska, to lay again. This is more likely due to physiological restrictions on egg production under the severe arctic conditions than to the short breeding season, because replacement of a nest lost at an early stage of incubation would not lead to a severe delay in nesting. Without the ability to renest, laying of multiple clutches is impossible. In temperate regions, however, lack of multiple clutches cannot be explained so simply as most waders do lay replacement clutches in case of nest failure.

Second, it is generally accepted that the species-specific clutch sizes are ultimately adapted to average level of the food supply, either through the average capacity of the parent birds to feed their young or the average amount of food available for the laying female (e.g. LACK 1966, 1968, KLOMP 1970). Furthermore, many birds are known to lay larger clutches when food at the time of laying is plentiful, and vice versa (see also BENGTSON 1971). In principle, there is no difference if a bird lays, say, 8 eggs in one clutch or 4 + 4 eggs in two clutches in rapid succession. Hence, abundant food is to be expected to promote, and scarce food to restrain, the evolution of the rapid multi-clutch system.

Third, the amount of food available may be important not only at the time of laying but also during incubation. In all species laying multiple clutches, at least the first nest is attended by a single bird, and, as pointed out already by PITELKA, HOLMES & MACLEAN (1974), the one-adult incubation system can be successful only when food density is high. If food is scarce more time is needed for foraging, and prolonged absences from the nest could make the incubation insufficient.

The significance of high food supply for the evolution of a rapid multi-clutch system has been stressed above. However, *low* food supply may also lead to the same strategy. As pointed out by many authors (SELANDER 1972, GRAUL 1973, NETHERSOLE-THOMPSON 1973), low food supply may promote a reduction in female participation in parental duties, partly because an early departure by the female reduces competition for food, and partly because the female may lack the energy reserves needed to share in parental responsibilities after egg production. Although this is potentially an important step towards a rapid multi-clutch system, evolution can hardly proceed further as long as the availability of food for the laying female is low, but the situation will change if the species colonizes new regions or habitats with richer food resources. Now the females, freed from parental duties, are able to lay additional clutches and the multi-clutch system can evolve. But a prerequisite is, of course, that one adult is able to raise the brood unaided, and this is not so if food is *too* scarce in the original area.

Of environmental factors other than food which may have played a role in the evolution of wader social systems, predation pressure is probably the most important. In wader populations where predation rates are high, there must be intensified selection for production of multiple clutches. ORING & KNUDSON (1972), GRAUL (1973) and JENNI (1974) have all emphasized the significance of this factor in the evolution of rapid multi-clutch systems. Other possible factors (interspecific competition, diversity of habitat, climatical conditions, etc.) are mainly indirect, influencing habitat selection and so the availability of food and predation pressure.

On the other hand, some adaptations in the breeding behaviour may have retarded the development of multiple clutches. Laying of more than one clutch is not possible without preceding weakening of pair bonds. But in the ancestral monogamous single-clutch system, there has been an opposite selective pressure towards the persistent pair bond because of its general advantages (cf. PITELKA, HOLMES & MACLEAN 1974). Once the pair bond has developed beyond a certain strength, the evolutionary way towards multiple clutches is blocked because the necessary "intermediate stages", i.e. females with looser pair bonds and weaker incubation drive, are not favoured by natural selection. This may be the explanation of the paradox that even species having potentially good qualifications for laying multiple clutches (high food supply, long breeding season, capability of renesting) have rarely evolved this system.

To conclude, the evolution of rapid multi-clutch systems has not followed a standard pathway in all species. Many different factors, both promoting and restraining, have been involved, and the combined effect of these counteracting selective forces has determined the direction of the evolution. It is significant that in none of the known species laying multiple clutches, except perhaps the American Jacana, have the mating systems reached the final stage of the evolution. In Temminck's Stint, for example, various exceptions to the normal schedule are common, and wide individual variation in breeding behaviour has been stressed also by HAYS (1972), ORING & KNUDSON (1972) and GRAUL (1973) with respect to the Spotted Sandpiper and Mountain Plover.

This suggests that the rapid multi-clutch system is a rather new breeding strategy and is not sufficiently advantageous to all species to become prevalent. It also may imply the existence of geographical differences in breeding strategies within the same species. Environmental conditions are often highly variable within a species' range, and what may be advantageous in one area may be disadvantageous in another. In Temminck's Stint, for instance, my studies have been carried out at the southern border of its range and concern an almost isolated population breeding on the coast of the Gulf of Bothnia. It is quite possible that future investigations on the arctic breeding grounds of the species, with a shorter breeding season and very different climatic and ecological conditions, will reveal a different mating system. Such a comparative study would be highly desirable.

Table 5. Clutch size and relation of egg weight to female body weight in wader species laying multiple clutches.

Species	Clutch size	Egg weight	Female body weight	Relative egg weight[1]	Relative egg production[2]	Author
Calidris temminckii	4	6.0	27.8	**21.6**	**86**	This study
Calidris alba	4	11.2	55.0	20.4	81	Schönwetter (1960—66)[4] Glutz et al. (1975)[5]
Tringa macularia	4	8.8	51.5	17.1	68	Oring *(in litt.)*
Charadrius montanus	3	15.6	106.8[3]	14.6	44	Graul (1973)
Eudromias morinellus	3	17.0	120.0[3]	14.2	43	Graul (1973)
Phalaropus lobatus	4	6.3	38.0	16.6	66	Schönwetter (1960—66)[4] Hildén & Vuolanto (1972)[5]
Jacana spinosa	4	8.3	160.9	5.2	21	Schönwetter (1960—66)[4] Jenni & Collier (1972)[5]
Rostratula benghalensis	4	12.5	126.0[3]	9.9	40	Schönwetter (1960—66)[4] Ali & Ripley (1969)[5]

[1] Egg weight as a percentage of female body weight.
[2] Clutch weight as a percentage of female body weight.
[3] Average of both male and female weights.
[4] Data on egg weight.
[5] Data on female body weight.

3\. *Adaptations related to the rapid multi-clutch system.* Theoretically, there are many possible ways of reducing the demands on the female caused by laying more than one clutch.

Reduced egg or clutch size. Production of smaller or fewer eggs consumes less energy, and one might expect reduced egg or clutch size in species exhibiting a rapid multi-clutch system, as claimed by Lack (1968), Oring & Knudson (1972), Graul (1973), Parmelee & Payne (1973) and Jenni (1974). This has been tested in Table 5. Temminck's Stint and Sanderling do not show any reduction in egg size when compared to other species of the same genus, contrary to what has been stated: "the very small egg of *Erolia temminckii* . . ." (Lack 1968, p. 219), "both Temminck's Stints and Sanderlings have unusually small eggs in relation to body size . . ." (Parmelee & Payne 1973). Ten other *Calidris* species, on which Schönwetter (1960—66) and Glutz et al. (1975) give the necessary information, have relative egg weights of the same order, ranging from 13 to 28 % and averaging 21.2 %. On the other hand, the Spotted Sandpiper has considerably smaller eggs than the three small European *Tringa* species, the Common Sandpiper *T. hypoleucos*, Wood Sandpiper *T. glareola* and Green Sandpiper *T. ochropus*, which have relative egg weights of 26.0, 22.5 and 19.4 %, respectively (Schönwetter 1960—66). The Mountain Plover and the Dotterel also have somewhat smaller relative egg weight than the other plover species listed by Graul (1973); the latter average 19.8 %. Likewise the eggs of the Red-necked Phalarope are rather small in relation to the body size, as in all phalaropes, but only the American Jacana and Painted Snipe show much reduced egg size.

As to clutch size, all but two of these

species lay the ancestral Charadrii clutch of 4 eggs. The Dotterel and Mountain Plover lay only 3 eggs, but a great number of other plover species which do not lay multiple clutches also have reduced clutches of 3 or 2 eggs (MACLEAN 1972). Hence, reduction of clutch size cannot be considered a general adaptation in species with rapid multi-clutch systems.

It seems clear why most wader species show little or no reduction in egg size. The smaller the relative size of the egg, the less food reserve it contains for the newly hatched young. For most species treated here the climatic conditions on the breeding grounds are very unpredictable, with frequent spells of adverse weather and concomitant shortage of food, so it would be a great risk for precocial young to hatch without sufficient food reserve. This risk does not affect the American Jacana and Painted Snipe, which live in a rich tropical environment with stable climatic and food conditions, and consequently these two species are the only ones with much reduced egg size.

That most wader species laying multiple clutches do not show a reduced clutch size is also easy to understand. If, on average, production of two clutches of normal size in rapid succession is too heavy a demand on the female, then a reduction in clutch size is a prerequisite for the evolution of a rapid multi-clutch system. By itself, however, a smaller clutch is merely a disadvantage, if the species is capable of producing the original clutch of 4 eggs, and so evolution cannot proceed along this line. Where reduced clutches occur in waders, they have not evolved to permit production of multiple clutches but in response to certain environmental factors, probably most often to the availability of food.

Prolonged laying interval between the clutches. One way to reduce the demand on females caused by successive clutches could be to lengthen the interval between them. Temminck's Stint has the shortest interval, only 2 to 4 days; about 5 days is involved in the Spotted Sandpiper, Red-necked Phalarope and Dotterel, 7 to 10 days in the American Jacana and 9 to 13 days in the Mountain Plover. In most of these species, the interval between the two clutches is about as short as is needed for egg-formation in waders in general (cf. HILDÉN & VUOLANTO 1972, p. 73). Hence, evolution has not led to a prolonged interval between clutches to facilitate the production of multiple clutches. The probable reason is that breeding season available for wader species in northern regions is very short, so that a delayed second nesting would be disadvantageous. The two species with the longest intervals are those with the southernmost breeding ranges and thus the longest seasons for breeding. In the Mountain Plover, the relatively long clutch-interval is also likely to be due to the poorer feeding conditions: its habitat, the shortgrass prairie, is less productive, on average, than those of the other species.

Delayed sexual maturity. Many bird species do not breed until two or three years old, probably because breeding at a younger age would be too heavy a strain for unexperienced birds (LACK 1966, 1968). As the laying of multiple clutches is a particularly strenuous breeding system, one would expect a delay in the age at which females first breed in species with this type of strategy.

In Temminck's Stint, however, females commonly breed when only one year old. One of these birds (F 25/1964, see p. 128) laid three successive clutches (12 eggs) within 16 days! So this species does not show deferred maturity. On the contrary, it starts breeding earlier than the single-clutched Dunlin, for instance, which usually breeds first when two years old (SOIKKELI 1970b).

As to the other species showing multiclutch systems, information on their age at sexual maturity is scanty. ORING & KNUDSON (1972) assume that advanced age at first breeding would be an adaptation to minimize strain on the female in these species, but they give no data in support. The unbalanced sexual ratio, with males predominating, shown to exist in populations of the Spotted Sandpiper (HAYS 1972, ORING & KNUDSON 1972) and the American Jacana (JENNI & COLLIER 1972, JENNI 1974), suggests that at least in these two species females start breeding older, on average, than males. This, in turn, makes the polyandrous system possible, more males than females being available. On the whole, however, waders that lay multiple clutches seem to breed for the first time at about the same age as single-clutched wader species.

Delayed onset of the male's incubation. A characteristic breeding adaptation of Temminck's Stint is the delay of the male's incubation for some days, during which he continues to display. Also at one Sanderling's nest, the male delayed the start of incubation for nearly six days (PARMELEE & PAYNE 1973).

The significance of this adaptation is easy to understand. If the males commence incubating immediately after clutch completion, they have no chance to increase the number of their offspring by fertilizing additional clutches. Also females would have difficulties to find second mates, with only those late to arrive or excess males available. This situation would lead to the type of polyandry found in the Spotted Sandpiper, Red-necked Phalarope and Dotterel. Hence, without the delayed start of incubation the whole breeding mechanism of Temminck's Stint would not be possible. Consequently, natural selection has favoured those males which have delayed the onset of incubation and thereby succeeded in fertilizing another set of eggs. Another possibility, found in the Mountain Plover (GRAUL 1973), is that the male maintains his sexual activity during the first days of incubation and tends the nest only sporadically.

A further possible advantage of the delay in the male's incubation is that the brood period is synchronized. For, as a result, the young in the nests incubated by the male and the female hatch almost simultaneously. The somewhat increased egg losses due to the prolonged incubation period apparently do not outweigh the selective advantages of the habit.

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Selostus: Lapinsirrin *Calidris temminckii* pesimäsysteemi

1. Tutkimus on suoritettu 1963—72 Harrbådan —Rummelön alueella Kokkolassa, missä pesii Suomen eteläisin pysyvä lapinsirrikanta (vuosittain 15—36 yks.). Pääosa pesistä on löydetty, lähes puolet jo munintavaiheessa (taul. 1). Aikuisista linnuista n. 80 % on värirengastettu

(yht. 85 yks.), poikasista lähes kaikki tavallisin renkain (yht. 323 yks.). Sukupuolet voi maastossa erottaa varmasti vain käyttäytymisestä, kädessä useimmiten painosta (taul. 2, kuva 2).

2. Kukin ♀ pariutuu peräkkäin 2 ♂♂:n kanssa ja munii pesyeen kummankin reviiriin. Pesyeiden aikaväli on vain 2—4 vrk. Vastaavasti kukin ♂ pariutuu peräkkäin 2 ♀♀:n kanssa ja hedelmöittää pesyeen kummallekin. Ensimmäistä pesyettä rupeaa hautomaan ♂, toista ♀. Molemmat huolehtivat myös poikueestaan yksin. Poikkeukset normaalista pesimäsysteemistä ovat melko tavallisia. Useimmat johtuvat ♂♂:n taipumuksesta moniavioisuuteen. Ne kosiskelevat jokaista reviiriinsä tullutta ♀:ta, ja monesti on saman ♂:n nähty yrittävän parittelua 2—3 ♀♀:n kanssa lyhyessä ajassa. Tämän seurauksena välistä 2 ♀♀ munii 1. pesyeensä samaan reviiriin, jolloin toinen aina jää hautomatta. Kerran 2 ♀♀ muni samaan pesään yht. 7 munaa. Kahdesti on ♀:n todettu munivan 3 peräkkäistä pesyettä. Uusintapesyeet tuhoutuneen tilalle ovat hyvin harvinaisia.

3. Naaraita on kahta tyyppiä: pesimäpaikalle uskollisia, jotka palaavat vuosittain samalle alueelle ja munivat sinne molemmat pesyeensä, ja kierteleviä, jotka vaihtavat pesimäaluettaan sekä molempien pesyeidensä välillä että vuodesta toiseen. Jälkimmäisiä on n. kolmannes ♀♀:sta. Koska tutkimusalue sijaitsee lajin pesimäalueen eteläreunalla, sieltä lähtee kierteleviä ♀♀:ta pois ennen 2. pesyeensä munintaa paljon enemmän kuin uusia saapuu tilalle; tästä syystä alueella on 1. pesyeitä selvästi enemmän kuin toisia (taul. 3).

4. Samantapainen pesimäsysteemi (kaksoispesintä), jossa ♀ munii kaksi tai useampia pesyeitä lyhyin välein, on todettu toistaiseksi 7 muulla kahlaajalajilla (*Calidris alba, Charadrius montanus, Tringa macularia, Phalaropus lobatus, Eudromias morinellus, Rostratula benghalensis, Jacana americana*), toisilla niistä säännöllisesti, toisilla tilapäisesti. Yksityiskohdissa näiden lajien pesimäsysteemeissä on kuitenkin paljon eroja.

5. Kahlaajien alkuperäisin pesimäsysteemi on yksiavioisuus, jossa parisiteet ovat kiinteät ja molemmat sukupuolet osallistuvat pesimistoimiin. Lukuisat muut systeemit ovat erilaistuneet tästä perustyypistä luonnonvalinnan kautta, sopeutumina erilaisin ympäristöoloihin ja lajien erilaisiin elintapoihin. Kaksoispesinnän kehitys on edennyt kahta päälinjaa: joko ♂ ja ♀ hautovat omia pesyeitään tai ♀ munii pesyeensä 2 ♂♂:lle eikä itse osallistu jälkeläisten huoltoon (kuva 4).

6. Kaksoispesinnän valintaetuna on jälkeläismäärän kasvaminen. Haittoina ovat haudonnan ja poikashoidon jääminen yhdelle emolle, parisiteiden heikentyminen ja lisääntynyt rasitus ♀:lle, jotka kaikki joko huonontuneen pesimätuloksen tai ♀:n lyhentyneen eliniän kautta voivat pienentää jälkeläisten määrää. Kaksoispesinnän kehittyminen tai estyminen riippuu näiden vastakkaisten valintatekijöiden keskinäisestä voimakkuudesta.

7. Kirjoittajan käsityksen mukaan kaksoispesintä on voinut kehittyä vain oloissa, missä ravintoa on runsaasti tarjolla munintaaikana. Useimmista tämän pesimäsysteemin omaksuneista lajeista käytettävissä olevat tiedot osoittavatkin näin olevan. Muista kaksoispesinnän kehittymiseen myötävaikuttaneista ympäristötekijöistä suuret pesä- ja poikastappiot ovat ilmeisesti tärkeimmät. Parisiteiden lujittuminen taas on voinut estää kaksoispesinnän kehittymisen sellaisillakin lajeilla, joilla olisi ollut tähän riittävät edellytykset.

8. Lopuksi tarkastellaan kaksoispesintään liittyviä muita sopeutumia. Munan koko on pienentynyt jonkin verran neljällä ja huomattavasti kahdella lajilla, kun taas kahden lajin munan koossa ei ole eroa saman suvun muihin lajeihin verrattuna (taul. 5). Pesyekoko ei ole yleensä pienentynyt, vaikka tämä vähentäisikin ♀:n rasitusta. Myöskään pesyeiden aikaväli ei ole kehittynyt juuri pitemmäksi kuin munien muodostaminen vaatii. Kaksoispesintään sopeutuneiden lajien ♀♀ eivät näytä saavuttavan sukukypsyyttä myöhemmin kuin yhden pesyeen munivien lajien ♀♀. Selvä sopeutuma kaksoispesintään on sitä vastoin lapinsirrillä todettu ♂:n tapa viivyttää haudonnan alkamista muutamia päiviä, jona aikana se säilyttää soidinvireensä ja pystyy hedelmöittämään toisen ♀:n pesyeen.

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