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Polyterritorial polygyny in the Pied Flycatcher Ficedula hypoleuca — evidence for the deception hypothesis

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We scrutinize the arguments that can be used to explain the evolution of polyterritorial polygyny in the Pied Flycatcher. In this species, secondary females of polygynous males have highly reduced breeding success in comparison with simultaneously laying monogamous females. This reduction in offspring numbers will not be compensated for in future generations as proposed by the "sexy son" hypothesis. The polyterritorial polygyny in the Pied Flycatcher cannot be described in terms of female choice models (the Orians-Verner model and its modifications). On the present evidence the deception hypothesis (i.e. secondary females are unaware of male mating status at mating) is the most likely explanation of polyterritorial polygyny in this species.

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1. Introduction

Polyterritorial polygyny in the Pied Flycatcher Ficedula hypoleuca was first detected and described in detail by von Haartman (1945, 1951) over thirty years ago. Only much later did Verner (1964), Verner & Willson (1966) and Orians (1969) propose the "polygyny threshold" model as a general explanation of polygyny in monoterritorial bird species. This model, however, did not seem to be applicable to the polyterritorial Pied Flycatcher (von Haartman 1969a, Wittenberger 1976, Alatalo et al. 1981, 1982a). In this paper we will review the various hypotheses that could explain polygyny in the Pied Flycatcher and we will summarize our tests of these hypotheses. Most of the data gathered during the years 1979-1982 around Uppsala in central Sweden have already been published in a series of papers (Alatalo et al. 1981, Lundberg et al. 1981, Alatalo et al 1982a, 1984a, 1984b). We will also present some new data, in particular concerning a population nesting in natural holes that was studied in spring 1983.

2. Polyterritorial polygyny

Apart from von Haartman's (1945, 1951, 1956) studies in Finland, polyterritorial polygyny in the Pied Flycatcher has been described by Creutz (1955), Curio (1959) and Winkel & Winkel (1984) in Germany and by Askenmo (1977) and Silverin (1980, 1983) in Sweden. In central Sweden Pied Flycatchers arrive at the breeding grounds from late April onwards. On average, males arrive several days before females, but the earliest females arrive before the latest males. Each male occupies a small territory consisting of one or several nest boxes, which are demonstrated to visiting females. If a prospecting female accepts one of the nest boxes offered, breeding activities will begin promptly. Usually the female lays her first egg within 5-10 days of arrival. After having paired up with a female, males do not normally sing as loudly as they did before pairing and they accompany the female most of the time before egg laying. Roughly at the time the first egg is laid, many males establish a secondary territory where they again begin to sing loudly in an attempt to attract a secondary

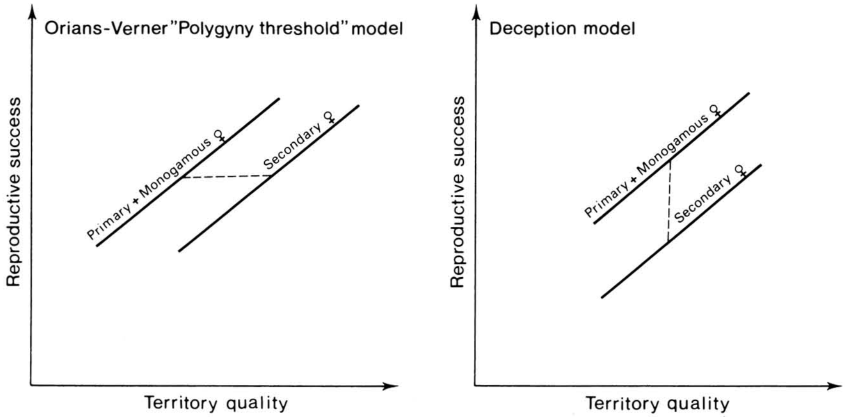

Fig. 1. Schematic presentation of the polygyny threshold model (1a) where females, being "aware" of territory quality and male status, use reproductive success as the criterion for mate choice. In the deception model (1b) females are unaware of male mating status and use only territory quality for mate choice and hence secondary females achieve a lower reproductive success than concurrent primary and monogamous females (see broken lines as examples of reproductive success of concurrent females of different status).

female. Some males succeed in this enterprise but they subsequently return to the primary female to aid her in feeding the nestlings. Males may help the secondary female too, mainly after the young from the primary nest have fledged or if the primary and secondary nests are situated near each other. A few males may attract three females (Askenmo 1977, Winkel & Winkel 1984), but we have observed only two cases of trigyny.

When using the term polygyny we only refer to social and not to sexual relations. Males are highly promiscuous and cuckoldry is common. This leads to multiple paternity within broods and the most likely father of the young in a brood, apart from the male at the nest, is the nearest neighbour (Björklund & Westman 1983, Alatalo et al. 1984a).

3. The deception hypothesis — a short description

von Haartman (1969a) pointed out that it is unlikely that prospecting secondary females are aware of the presence of the primary female at mating. This violates a crucial assumption of the Orians-Verner polygyny threshold model (Wittenberger 1976, 1979), namely that secondary females know the male's mating status. We have proposed a "deception" hypothesis to account for the evolution of polygyny in the Pied Flycatcher (Alatalo et al. 1981, 1982a, 1984b, 1984c). At mating, females cannot use male mating status as a criterion in mate choice and hence they are deceived into accepting a less favourable situation as a secondary female. Polyterritoriality enables deception and is likely to have evolved to increase the chances of males becoming polygynous. Females make use of territory quality as their major criterion of mate choice and hence a situation arises where secondary females suffer lower breeding success than do monogamous and primary females mating at the same time (Fig. 1). Females might be able to avoid polygynous males through longer courtship periods, which they cannot afford since the suitable breeding season is very short and breeding success declines rapidly with time (see Alatalo et al. 1981).

4. Testing the alternative hypotheses

4.1. The Orians-Verner polygyny threshold model

Breeding success

The basic premise of this model is that females are aware of male mating status and that they mate with already-mated males only if they can achieve at least as high a reproductive success as monogamously mated females mating at the same time (Verner 1964, Verner & Willson 1966,

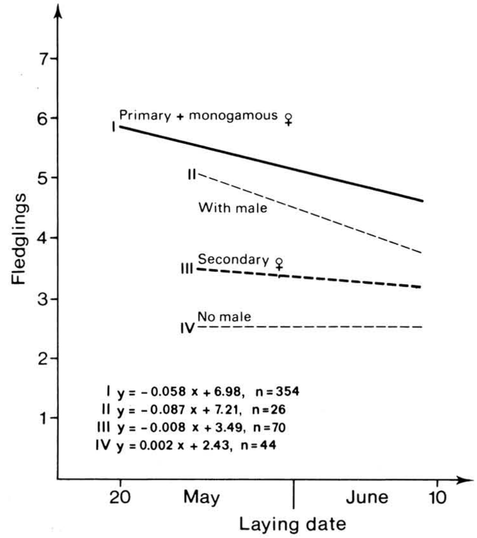

Fig. 2. Breeding success of secondary females in comparison to simultaneously laying monogamous plus primary females. Secondary females are divided into females which received some male assistance and females which had to raise their broods single-handedly.

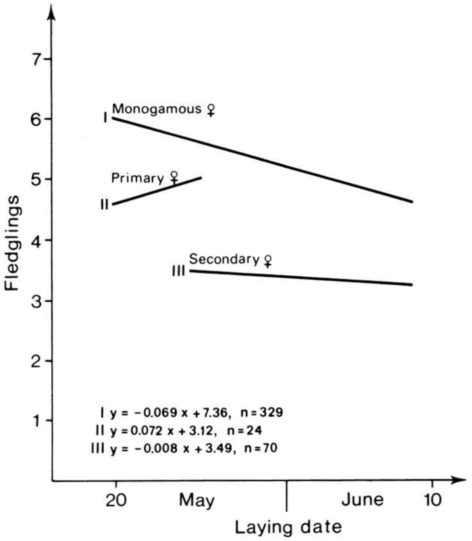

Fig. 3. Female breeding success in relation to laying date.

Orians 1969, Wittenberger 1979, Garson et al. 1981). Secondary females, thus, can compensate for reduced male assistance by availing themselves of high quality territories (Fig. 1a). Polygyny arises only if some males are able to monopolize the best breeding sites so that a portion of males remain unmated on very poor territories.

von Haartman (1951, 1969a), Curio (1959), Askenmo (1977) and Winkel & Winkel (1984) have already found a low breeding success for secondary Pied Flycatcher females. The crucial test is to compare breeding success of secondary females to that of monogamous and primary females combined (Alatalo et al. 1981, 1984b). According to our data from 1979 to 1982, secondary females raise only 64.8 % as many offspring to the age of fledging as do other females (Alatalo et al. 1984b, Fig. 2). To make an appropriate test, we standardized the offspring number in each nest by dividing it with the value given by the regression equation that describes the offspring number in monogamous and primary nests against laying date. Standardization eliminates the general seasonal decline in breeding success ensuring that we compare breeding success in simultaneous nests. The standardized values do differ highly significantly between the two groups of females (Mann Whitney U-test, $z = 7.72$, $P < 0.001$).

Figure 3 summarizes breeding data for all three types of females separately. For monogamous females there is a seasonal decline in fledgling numbers, early laying females producing on average six young but later females, laying in June, less than five. For secondary females the corresponding figure is just over three (64.4 % compared with monogamous females) rather independently of laying date. Now we also have data which show a reduced breeding success for primary females (= 80.9 % in relation to simultaneous monogamous females, $U = 3.75$, $P < 0.001$). Primary females produced five nestlings, on average, whereas early monogamous females had one nestling more. Observe that the positive regression coefficient for primary females in the figure does not differ significantly from zero. In general, polygynous males first help their primary female in raising the young, but later many of them also visit secondary nests and therefore primary nests receive, at the end of the nestling period, less male aid than do monogamous nests (Alatalo et al. 1982a). Hence, it is not only secondary females that suffer from reduced male assistance but primary females too. Primary females obviously cannot forecast the possible second pairing of the male later on, and hence not even they can make the choice that is implied in the Orians-Verner model. The above analyses include data from both deciduous and coniferous forest which is appropriate since Pied Flycatchers of the two habitats do not constitute separate populations. We have observed several times birds changing habitat between years and polygynous males having their females in different habitats.

So it becomes clear that secondary females suffer highly reduced breeding success in relation to concurrently laying monogamous and primary females. Clearly this is not in agreement with the predictions of the Orians-Verner polygyny threshold model (the continuous model of Wittenberger 1979). We have also previously, on similar grounds, rejected this model as a possible explanation for the evolution of polygyny in the Pied Flycatcher (Alatalo et al. 1981, 1982a, 1984b).

Polygyny frequency

According to the Orians-Verner model some males monopolise resources which are essential for females. In Pied Flycatchers the most essential resource for females is likely to be a suitable nest site. Hence, if the Orians-Verner model is true, we should expect polygyny to occur most frequently if suitable nest sites are in short supply and more in deciduous habitat which, in our study area, is more suitable for Pied Flycatchers than the coniferous habitat (see Lundberg et al. 1981).

In deciduous forests, when nest boxes are placed widely scattered in low densities (<1/ha) and all or nearly all boxes become occupied (90-100%), the polygyny frequency is low (Table 1). When nest boxes are offered in "excess" (>50% of boxes empty), the estimated polygyny frequency is somewhat higher (11.3% of nests being secondary) but the difference between the two types of deciduous nest box areas is not significant ($\chi^2 = 0.53$, $P > 0.10$).

In coniferous (pine-dominated) forests where Pied Flycatcher densities in general are lower than in deciduous forests (see Lundberg et al. 1981) only a low frequency of polygyny is observed if nest boxes are in short supply (Table 1). However, when nest boxes are provided in excess in this habitat (though still being more widely scattered than in the high density situation in the deciduous habitat), the polygyny frequency becomes significantly higher (Fisher's exact probability test, $P < 0.01$). Almost 40% of the nests belonged to secondary females in this situation (see also Askenmo 1977 for high polygyny frequency in coniferous stands). It is noteworthy that males sometimes had their secondary female in the coniferous forest while the primary female was in a deciduous forest. Furthermore, trigyny is likely to occur regularly in coniferous habitats (we have incorporated the third females among secondary females), but it is very difficult to observe. Askenmo (1977) recorded four cases of trigyny in coniferous forest and we observed one trigamous male in that habitat (and one in deciduous forest).

Table 1. Polygyny frequency in deciduous and coniferous habitat at different nest box densities.

	Breeding pairs/ha	Number of males	% secondary territories
Deciduous forest			
Boxes in shortage	<1	44	6.8
Boxes in "excess"	1-3	212	11.3
Coniferous forest			
Boxes in shortage	<0.5	16	6.3
Boxes in "excess"	0.5-1	71	39.4

In order to study the influence of nest site distribution we have put up groups of two to nine nest boxes in deciduous forest with nest boxes being very near each other (10-50 m) and the distance between groups being much longer (>100 m). In such a situation males should have maximal possibilities to monopolise several nearby nest boxes. If the Orians-Verner model was applicable and males after having attracted a female were to choose the second best nest box, irrespective of distance, polygyny should be faciliated within these groups (boxes being of similar quality and close to each other) in comparison to our other areas where nest boxes are regularly spaced. If males choose nest boxes in descending quality order we should expect at least as high polygyny frequency in these experimental groups as in our other deciduous areas. However, among 52 nestings we never observed a male having two females within the

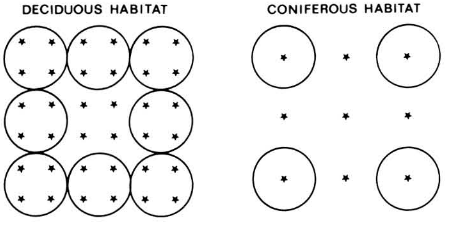

Fig. 4. Schematic presentation of primary territories (circles; crosses indicate nest boxes) of Pied Flycatcher males to illustrate that there is more space available for secondary territories in coniferous than in deciduous forest.

same group of nest boxes. This is significantly less than expected (Fisher exact, $P < 0.01$) and implies that a long distance is required for the male Pied Flycatcher to attract a second female.

If nest boxes are provided in excess, polygyny frequency is much higher in poor coniferous than in rich deciduous habitat, which is opposite to the prediction derived from the Orians-Verner model. Why is this? In deciduous forests with nest boxes in excess (nest boxes 30-40 m apart) the breeding density is high and there is little, if any, space between territories of adjacent Pied Flycatchers (Fig. 4). Males have access to several nest boxes within their territories but have difficulty in establishing a secondary territory. Even if Pied Flycatchers defend a rather small area around the nest (von Haartman 1956), it may include several nest boxes. Nest boxes that are close to an active nest (<50 m in deciduous and <100 m in coniferous forest) are less likely to be occupied by other flycatchers than nest boxes further away (Alatalo et al. 1982b, 1984c). In the high density coniferous situation male density is much lower and free nest sites occur between territories (Fig. 4). A further factor may be a reduced risk of cuckoldry by neighbours in the absence of the male if absolute density is lower. Thus, in the coniferous habitat males have better possibilities to take up secondary territories. In the deciduous habitat males can monopolise several nest boxes within their primary territory, but this does not encourage deception polygyny.

In the low density situation when nest boxes are in short supply, all boxes become occupied very soon after the arrival of males and males have very limited chances of establishing secondary territories at the time when they can leave their first female. It does not even help to have empty nest boxes very near the first female.

Altogether, polygyny frequency rises with the increased probability of males being able to establish secondary territories, that is, in situations where nest boxes are least monopolised and easily available to all males. It seems to be crucial that males, in order to become polygynous, can acquire really distant territories. In central Europe (Creutz 1955, Curio 1959) and in England (Campbell, in Lack 1966) polygyny frequencies have been reported to be comparatively low, 3-10%, which may be due to high breeding densities.

4.2. The "sexy son" hypothesis

This hypothesis was put forward by Weatherhead & Robertson (1979, 1981) and has been modelled further by Heisler (1981). Its general applicability has been questioned by Alatalo et al. (1981), Searcy & Yasukawa (1981), Wittenberger (1981) and Alatalo & Lundberg (unpubl.). The hypothesis is an extension of the Orians-Verner model, attempting to explain how secondary females, although producing fewer offspring than monogamous females, yet may acquire at least as high fitness. Sons of polygamous males are assumed to become polygamous themselves with a greater likelihood than other male offspring. These sons are termed "sexy" due to the attractive genes they possess. Järvi et al. (1982) proposed that the hypothesis may be applicable to the Pied Flycatcher.

Alatalo & Lundberg (unpubl.) analyzed this hypothesis and its applicability to the Pied Flycatcher in detail. In short, it is not likely that any observable reduction in initial breeding success may be compensated for by good genetic quality of the offspring. The "sexy son" hypothesis could work only under unrealistically high levels of beneficial mutations. We argue that variation in male mating success is largely caused by phenotypic variation and not by additive genetic variance.

In the Pied Flycatcher, nestlings of secondary females suffer from poor nutrition, having lower weights and shorter tarsi than young from monogamous nests. It is likely that they are more vulnerable to mortality directly after fledging than other fledglings that are fed by two parents, and hence fitness in terms of surviving young to adulthood is likely to be even less for secondary females than in terms of fledgling numbers. Furthermore, sons of secondary females are of low phenotypic quality (the short tarsus is an irreversible indication of poor quality), and therefore it is much more realistic to assume that they are less likely to become polygynous than sons of monogamous males which are in better condition and hence will be able to arrive early in spring to defend several territories. In fact, males with short tarsi appear to be least likely to become polygynous. Furthermore, we have estimated that heritability of male mating status should be at least 80% before the "sexy son" mechanism might make it beneficial for females to become secondary in the population studied by us. We have no information on heritability, but repeatability of male mating status between different seasons was only 23%. Since repeatability affords a maximum estimate of heritability we can confidently state that it does not pay at all for secondary females to accept this status. If they were aware of it at mating, they should avoid it.

4.3. Other "female-choice" hypotheses

With female choice hypotheses we refer to explanations where females are supposed to choose to become secondary even if they are instantly aware of their status. Observe that even in the case of the deception hypothesis, females are choosy in their mate selection (e.g. with respect to territory quality) but they do not deliberately choose to mate with an already-mated male.

Under some circumstances one can expect secondary females to have lower breeding success than monogamous females even though females, when pairing, were aware of male mating status and made the best choice among available alternatives (see Wittenberger 1979). For instance, if the sex ratio is female biased and no unmated males are available it would pay for females to become secondary if the alternative option is not to breed at all. In a special study area (12.0 ha deciduous woodland, see Alatalo et al. 1984c) where we individually marked all territorial males and monitored them throughout the breeding season, 5 out of 34 (= 14.7%) in 1982 and 4 out of 31 (= 12.9%) in 1983 remained unmated. Three (= 8.8%) and two (= 6.5%) males, respectively, succeeded in attracting a secondary female. For each date when a secondary mating occurred, there were 1-6 (average = 3.8) unmated males available within the area. The presence of unmated territorial males has also been established by von Haartman (1951) and Curio (1959). Thus polygyny in the Pied Flycatcher cannot be explained by female biased operative sex ratios.

Wittenberger (1979, 1981) has formulated the discontinuous (discrete) model as another "female-choice" type of the polygyny threshold model. In the original Orians-Verner model territory quality is assumed to vary continuously, but in the discontinuous case there is a gap in territory quality, mated males having high quality territories whereas unmated males inhabit poor territories that are never accepted by females. Males with intermediate territories are missing. In this case a situation may arise where secondary females have a lower breeding success than nearly simultaneously mated monogamous females (for details see Wittenberger 1981). In practice this means that territorial males are highly polygynous while other males do not even take up territories. This model, however, is not applicable to the Pied Flycatcher where there is no discontinuity in territory quality and unmated males defend territories. Furthermore, even if this model was applicable, one should expect secondary females to enjoy at least as high reproductive success as simultaneously laying monogamous and primary females, which is not the case.

One might speculate that secondary Pied Flycatcher females, although having low breeding success, would benefit either by increased survival or increased future reproductive success. Secondary females, however, are often more over-worked than females with male assistance (Alatalo et al. 1982a) and hence, if anything, are less likely to survive than other females. Neither will they remate with the same male as primary or monogamous females next year since they show very low mate and nest site fidelity (see von Haartman 1949, Alatalo et al. 1983).

4.4. The natural situation

Little is known about the behaviour of Pied Flycatchers breeding in natural cavities. One could argue that the provision of good quality nest boxes may create an artificial situation producing maladaptive male and/or female mating behaviours. The most likely conditions for such a situation to emerge are: 1) High quality nest holes are scarce in nature and late females should always accept a male that offers a good nest site (Järvi et al. 1982). Since such nest holes are scarce, males would have difficulties in finding secondary territories and polyterritorial polygyny should be infrequent. 2) The average quality of a natural nest hole is much lower than of a nest box. Being a secondary female in a nest box could, therefore, grant a higher reproductive success than being monogamously mated and having a natural nest site. Hence females might choose to become secondary in a nest box. Nilsson (1984) studied Pied Flycatchers in natural cavities in southern Sweden and the average number of fledglings in them (3.25) was significantly lower than in nest boxes (4.67).

In the breeding season of 1983 we studied Pied Flycatchers in a 40 ha deciduous forest north of Uppsala (Andersby), only little affected by forestry and far from any nest box areas. Details of this area, its vegetation and land use are given e.g. by Larsson (1971) and Hytteborn (1975).

We found 21 Pied Flycatcher nests (0.5 females/ha). Three of the females were secondary (= 14.3%) and at least 12 out of 18 (= 67%) mated males were polyterritorial. Males were defined as polyterritorial if they were observed singing in another territory after having attracted a female in the first territory. It is possible that some of the "monoterritorial" males had a secondary territory outside our study area. No males attempted to attract another female in the main territory, where they stopped singing after the arrival of the female. The distance between the primary and secondary territories varied between 80 and 540 m with a mean of 300 m. The degree of polyterritoriality in the natural area was certainly higher than is the case in our high density nest box areas (Alatalo & Lundberg, unpubl.). With nest boxes in excess in coniferous forest we have found polyterritoriality of the same or even higher magnitude as in the natural area. The distance between territories of polyterritorial males among naturally breeding flycatchers were longer than in our nest box areas (median = 150 m, Fig. 5).

Our data on reproductive success of pairs breeding in natural nest holes are limited so far but monogamous plus primary females produced, on average, 5.2 fledglings per pair (n = 18). The median egg laying time for these pairs was 25 May. The corresponding figure in nest box areas during four years is 5.4 (n = 354) while secondary females breeding in nest boxes raise an average of 3.3 offspring (n = 70).

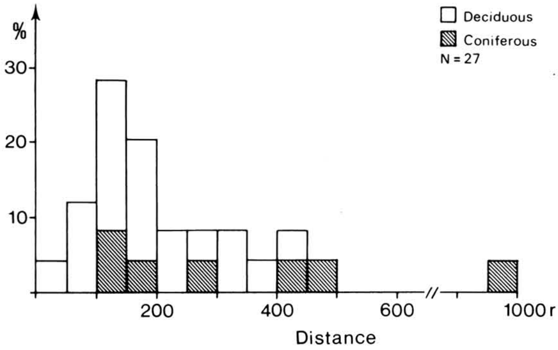

Fig. 5. Distance between the primary and the secondary female in nest box areas.

Our preliminary results do not support the two hypotheses mentioned in the beginning of this section. Males are highly polyterritorial in natural areas and it will not pay females to become secondary in a nest box compared to becoming monogamously mated in a natural nest hole. In any case, the presence of unmated males in nest box areas makes it difficult to understand why a female should "choose" to become a secondary mate in artificial nest sites. Moreover, if our second alternative hypothesis, i.e. secondary females in nest boxes have higher reproductive success than monogamous females in natural nest sites, is true, one would not expect to find so many secondary nests in natural cavities All three secondary females in the natural cavities were very seldom aided by the male and only one produced any fledglings at all. There are also several other objections to the first hypothesis that females should blindly accept a male with a good quality hole. If this was true, females should take the first nest box presented by any male in our nest box areas. This is not the case, for we have seen (as did von Haartman 1956) females visit several males before making a choice. Male assistance in feeding nestlings presumably is equally crucial for birds breeding in natural or in man-made cavities, and the selection pressure upon females to avoid already-mated males, if they were aware of the male status, should also operate under natural conditions.

In conclusion, we cannot find any support for the idea that the provision of nest boxes should produce maladaptive male and female behaviours, although nest boxes may affect breeding success in a positive way (see Nilsson 1984). High densities of nest boxes apparently suppress polygyny frequency in deciduous forests because males have difficulties in finding free secondary territories (but they do possess empty nest boxes near their primary female).

5. The deception hypothesis

5.1. Why are males polyterritorial?

Female-choice models, i.e. females deliberately choosing to become secondary since it is the best option available, cannot explain polygyny in the Pied Flycatcher. The deception hypothesis, according to which females are unaware of male mating status at mating, remains the most likely explanation. Polygynous Pied Flycatcher males have their two females in separate territories which enables them to practice male deception. One may ask whether polyterritoriality evolved in the first place to facilitate deception or if there are other factors that favoured the evolution of male polyterritoriality. In the latter case, males could be regarded as "honest deceptors" in the sense that polyterritoriality evolved in response to something else while female ignorance of the males' mating status helped in attaining secondary females.

We can suggest four possible mechanisms that alone or in concert could give rise to male polyterritoriality: 1) Female-female aggression, which has been suggested to be important in restricting polygyny in monoterritorial birds (von Haartman 1969a, Yasukawa & Searcy 1982). In fact, we have observed a few cases of aggression between a primary and a prospecting secondary female or between two neighbouring females mated to different males (Alatalo, Lundberg & Ståhlbrandt, unpubl.). Such confrontations never occurred further than 50 m from a female's nest. von Haartman (1956) observed aggression only between females trying to settle in the same nest box. It is difficult to decide whether a primary female can actually prevent a secondary female from occupying a neighbouring nest box or whether the prospecting female, as a result of the agression from the primary female, might realize that the male is already-mated and, therefore, will leave. Furthermore, when the first female is laying (developing eggs might be damaged during fighting) and/or incubating, her possibilities of driving other females are very limited indeed. Female-female aggression may be of some importance at very close distances, but even this remains to be proven. Of course, it is in the interest of the primary female to prevent her male from attracting another female but, given that the deception hypothesis is the explanation for most cases of polygyny in the Pied Flycatcher, prospecting secondary females should give up on the discovery of the presence of the first female. Certainly, female-female aggression cannot explain the relatively long distances between primary and secondary nests that are usually observed.

2) Males take up distant territories to avoid competition for food between his two females. We do not find this hypothesis plausible at all since males do not defend feeding territories but merely the nest site (von Haartman 1956). Monoterritorial males should be able to defend a larger total area than birds having two distant territories, one of which is frequently left unguarded. After the male leaves his first territory to establish another, other males can easily occupy nest boxes next to the one occupied by the primary female. Hence she will suffer food competition with other Pied Flycatchers. Distances between nests of different males can be very short (20-30 m observed in many cases by us). Altogether, long distance polyterritoriality is likely to make the food situation at the primary and secondary nests worse, because the longer the distance the less frequently can the male feed at each nest.

3) Males take the best available nest hole irrespective of its distance from the primary nest (see Meier 1983). Because we provide good quality nest boxes in excess, each male is likely to have favourable nest sites very near to the primary nest. In each territory males can defend several nest boxes before mating (von Haartman 1956, own data), since to have many boxes to offer to a prospecting mate should increase the chances for her of finding an acceptable one. Therefore, nest boxes near an active flycatcher nest are more likely to remain vacant than nest boxes further away (Alatalo et al. 1982b). Furthermore, the fact that males succeeded in attracting the primary female to their first territory implies that the local environment is of good quality.

There are important factors that would favour monoterritoriality if monoterritorial males would have some chances of becoming polygynous. Polyterritoriality is likely to increase the risk for cuckoldry (von Haartman 1951, Björklund & Westman 1983, Alatalo et al. 1984a). With short distance between nests males would more easily be able to assist in nestling care at both nests and nearby nest sites are also more easy to defend than distant ones.

It seems, then, unlikely that a lack of suitable nearby nest holes is the primary factor behind the evolution of the polyterritorial behaviour of the Pied Flycatchers. Males did not become monoterritorially polygynous even in situations where several nest boxes were provided in small groups (see section 4.1.2.). It might be that under natural conditions males are sometimes forced to move long distances to find a second hole. However, since suitable holes appeared to be patchily distributed in our natural study site, possibilities for monoterritoriality should exist. For instance, after one male in our "natural" area left the primary female for a second territory, another male appeared and attracted a female to a hole that was only 20 m from that inhabited by the primary female of the first male.

4) Males are polyterritorial to hide the fact that they are already mated (Alatalo et al. 1981, 1982a). In this case long distance between nests should be important for the male's prospects. Figure 5 (see also von Haartman 1956) summarizes the distances between primary and secondary nests in our nest box areas. Observe that we miss most of the long distances because our study areas are usually less than 10 ha. The maximum distance between primary and secondary territories known to us is 3.5 km (Silverin 1980). The great majority (85 %) of distances are over 100 m and many other nests of Pied Flycatchers are usually in between the primary and secondary nest (see also Alatalo et al. 1982a). According to our observations, females usually stay very close to their nest once they have settled there and in deciduous forest they usually stay within 50 m of the nest (Alatalo, Lundberg & Ståhlbrandt, unpubl.). With present evidence, polyterritoriality is likely to have evolved mainly to faciliate female deception by males.

5.2. Is polygyny always due to deception?

Occasionally males may have two females within the same territory. In our areas the distance between primary and secondary nests in four cases was less than 100 m. Von Haartman (1969b) once observed two females breeding in the same nest and Creutz (1955) describes a few such cases. Hence, not all secondary females are unaware of their secondary status at mating. One of the cases of short inter-nest distance in our studies apparently came about when a male disappeared (died?) a few days after pairing with a female. At this stage a neighbouring, already-mated, male began to consort with and paired with the female who was already building the nest. In another case a female deserted a nest that was completed but with no eggs, possibly because she was captured by us. She joined another male who already had a female, and began egg laying rapidly. In this case, the female must have been stressed to find a nest quickly, since eggs were already under formation. In a third case, the distance between nests was nearly 100 m and the primary and secondary females probably did not meet until several days after the secondary female arrived. These birds were observed by us daily, in a special study. In the fourth case the distance was 50 m and the male attracted a secondary female during the morning hours while the primary female was laying in her nest. Later on during the day the primary female was seen to be apparently aggressive towards the secondary

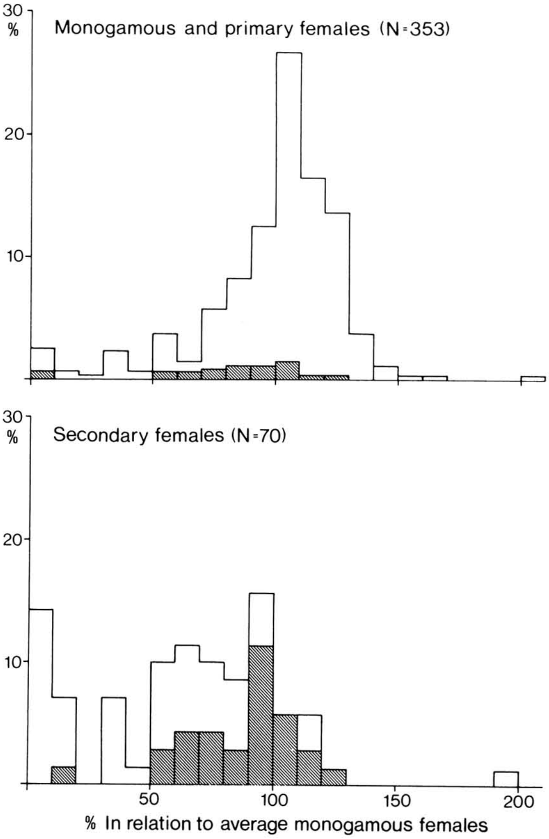

Fig. 6. Breeding success of different females in proportion (%) to concurrently laying monogamous females as given by the regression equation in Fig. 3. Shaded columns denote primary females in the top figure and secondary females with some male aid in the bottom figure.

female, who, nevertheless, stayed to breed. In this case the secondary female presumably was "aware" that the male was already paired.

Figure 6 illustrates the great variability in the breeding success of secondary females. What is interesting is that some secondary females (14%) enjoy at least as high breeding success as concurrently laying monogamous and primary females. These females did not lose anything by accepting already-mated males. The great variability in the breeding success of secondary females arises partly because some of them will be aided, more or less, by their males in brood care whereas others have to manage singlehandedly (Fig. 2). If secondary females were able to realize beforehand that they were going to receive some assistance by their male, it is possible that they could become polygynous in the way postulated by the Orians-Verner model. In particular, males that have their two nests near each other are likely to help at both nests and only in such situations may secondary females actually be aware of the males' status. Thus, a small proportion of polygynous matings with short distances between primary and secondary nests may be explicable in terms of the Orians-Verner polygyny threshold model. We wish to stress, however, that in the Pied Flycatcher polygyny, in general, cannot be explained by the Orians-Verner model and female deception seems to be the primary explanation of polygyny of this species.

5.3. From the female's viewpoint

Secondary females lay a slightly reduced clutch (Fig. 7) in comparison to simultaneously laying monogamous females (*U*-test, $z = 2.39$, $P < 0.05$). Reduced clutch size should be optimal for secondary females if they are already aware of their mating status before the end of the egg-laying period. Not all secondary females reduce their clutches and the average clutch size of secondary females presumably is not optimal in relation to expected fledging success since many young die in these nests. It is noteworthy also that primary females, possibly for the same reason, have significantly smaller clutches than simultaneously laying monogamous females (*U*-test, $z = 2.41$, $P < 0.05$; Fig. 7). It is to be stressed that there are no differences in age or size in concurrently laying females of different mating status. Thus, secondary females are not poor quality females and experimentally widowed monogamous females did as bad, or worse (because of no male aid at all), in raising the offspring as true secondary females (Alatalo et al. 1982a).

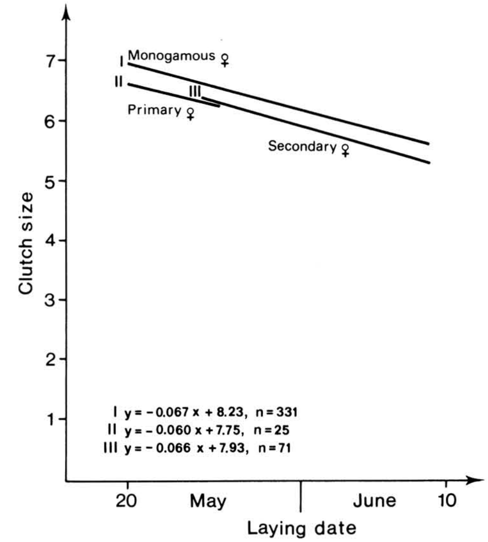

Fig. 7. Clutch size of females of different status in relation to laying date.

But why do secondary females not desert their clutch and search for a new male? We made a crude simulation (Fig. 1 and 4 in Alatalo et al. 1981) to assess the prospects for a deserting female and found that desertion would not be profitable for her because of the rapid seasonal decline in reproductive success. By now we have more data and the maximum delay a secondary female can afford to still retain her fledgling number if she is to leave her first (bigamous) male and search for a new one ($= t_c$ in our fig. 1 in Alatalo et al. 1981) can be estimated, for the earliest secondary females, at 15 days. This means that it could pay the female to desert her secondary status if she could remate within 15 days. However, such an analysis overestimates the prospects for a deserting female since there are other factors that would reduce her fitness. Thus, for example, late breeding females (as secondary females are) do not renest in the case of nest failure as the breeding season is very short. Besides losing renesting possibilities, late breeding may also result in delayed moulting and migration. Also, desertion of a nest may not easily arise if polygyny is relatively rare (15% in this study) and, in general, raising offspring must be strongly favoured by natural selection (compare for example the maladaptive behaviour of raising parasitic offspring). In summary, under the given circumstances secondary Pied Flycatcher females may behave in an optimal way and so make the best of a bad job.

Only greatly prolonged courtship periods would possibly allow females to discover male status and avoid becoming secondary. But females arrive late at the breeding areas and are in a hurry to start breeding. Prospects for successful breeding rapidly decrease with the progress of the breeding season and females are pressed for time. In the conflict between the sexes, circumstances favour males at the expense of females in the Pied Flycatcher.

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