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Polygyny in three temperate forest *Passerines* (with a critical reevaluation of hypotheses for the evolution of polygyny)

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During a four-year study carried out in primaeval stands of the Białowieża National Park (E Poland) a regular occurrence of polygyny in *Phylloscopus sibilatrix*, *Phylloscopus collybita* and *Troglodytes troglodytes* was recorded. The polygynous males were usually bigamists; trigamy was exceptional. All females a polygynous male obtained settled in the same territory. The polygynous birds were recorded almost exclusively in optimal (= high-density) habitats. Proportion of polygynous males in these habitats varied considerably between years, ranging from 0 to 40%. Mating success of individual males varied among seasons as well. Primary and secondary females settled often at the same time or only 1–2 days apart. Production of young per female in polygynous groups was not lower than the production of females mated to monogamous males.

The testability of polygyny threshold model is questioned. It is argued that current models dealing with female choice are insufficient to explain the evolution of polygyny. This is, because the settling females have to make a whole series of decisions, they have not only to choose mates but also habitats and geographical areas in which to breed. Choices made on the latter levels may be as important as mate choice in deciding if polygyny will occur. Monopolization of access to females by males can result in the appearance of polygyny even if it is detrimental to females. A model showing how differences in female and male habitat distribution (ideal free and ideal dominance, respectively) can lead to locally skewed sex ratios and occurrence of facultative polygyny, is presented. It is stressed that in order to explain the evolution of the resource defence polygyny one has to study simultaneously reproductive options available both to the females and to the males, as well as a whole set of ecological factors influencing the monopolizability of habitats by the males and costs of polygyny to the females.

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Полигиния у трех видов воробьиных птиц (с критическим обзором гипотез, касающихся эволюции полигинии)

В результате четырехлетних исследований, проводимых в первичных древостоях Беловежской пущи (вост. Польша), было констатировано, что у *Phylloscopus sibilatrix*, *Phylloscopus collybita* и *Troglodytes troglodytes* регулярно наблюдается полигиния. Полигинные самцы были обычно бигамистами, тригамия встречалась как исключение. Все самки полигинных самцов поселялись на одной и той же территории. Полигинные самцы констатировались почти исключительно в оптимальных биотопах (= с высокой плотностью). Процентное содержание полигинных самцов в этих биотопах было очень изменчиво и колебалось от 0% до 40%. Успех парования отдельных самцов

изменялся по годам. Первые и вторые самки полигинных самцов часто поселялись одновременно или с интервалом в 1–2 дня. Продукция молодых у самок из полигинных групп была не ниже, чем продукция самок, спарившихся с моногамными самцами.

Выдвигается мнение о возможности верификации модели „порог полигинии". Доказывается, что современные модели, касающиеся выбора партнеров самками не достаточны для выяснения эволюции полигинии по той причине, что поселяющиеся самки вынуждены выбрать не только самца, но также биотоп и соответственный географический регион, в котором они поселятся. Выбор на этих этапах может быть так само важным, как выбор самца, для решения о том, будет иметь место полигиния или нет. Монополизация доступа к самкам со стороны самцов может вести к полигинии, не смотря на то, что она будет вредна для самок. Представлена модель, указывающая на то, каким образом различия в распределении самцов и самок по биотопу (соответственно идеально доминирующее и идеально независимое) может вести локально к появлению количественного преимущества самок в популяции и полигинии. Подчеркнуто, что для выяснения эволюции полигинии, основанной на защите ресурсов, необходимо исследовать одновременно оптимальные возможности размножения, доступные для каждого пола, как и весь комплекс экологических факторов, влияющих на возможность монополизации биотопов самцами и последствия, которые несут самки.

INTRODUCTION

This paper constitutes an outgrowth of a much broader project on the breeding ecology and behaviour of *Phylloscopus sibilatrix*, *Phylloscopus collybita* and *Troglodytes troglodytes* in a primaeval temperate forest (Wesołowski 1980, 1981a, 1981b, 1983, 1985, Piotrowska and Wesołowski in press).

Its first part is devoted to documentation of polygyny in the species studied and a description of factors which could influence its occurrence.

Its second part, the discussion, does not consist only of comparisons of my data with theoretical predictions and findings of other students, but it also contains a critical reevaluation of current theoretical concepts. This is because, when attempts to explain the patterns observed in the Białowieża Forest with

the existing hypotheses had given unsatisfactory results, I felt it necessary to review the theory itself and to propose a theoretical framework broad enough to encompass my findings as well.

STUDY AREA AND METHODS

This study was carried out in the Białowieża National Park situated in the middle of the extensive (1250 sq km) Białowieża Forest in eastern Poland. The whole area of the Park (47.5 sq km) is a strictly protected nature reserve. The last fragments of primaeval lowland temperate forest are protected here (Faliński 1977, Tomiałojć *et al.* 1984).

In order to assess possible effects of habitat on mating success, observations were collected in parallel in two different plots. One of them, plot K, was covered mostly with swampy forest of the ash-alder type (*Circaeo-Alnetum*, tree-stand dominated by ash *Fraxinus excelsior*, alder *Alnus glutinosa*, and spruce *Picea excelsa*) but it also contained drier fragments covered with oak-hornbeam stands (*Tilio-Carpinetum*, tree-stand dominated by hornbeam *Carpinus betulus*, lime *Tilia cordata*, oak *Quercus robur*, continental maple *Acer platanoides* and spruce). The study started in 1976 in 12 ha part of this plot and was continued in 23 ha in 1977–79. The second plot-C-48 ha in size was covered with oak-hornbeam forest. For *T. troglodytes* and *P. collybita* observations were collected within the whole of plot C, but due to much higher numbers of *P. sibilatrix*, a 24 ha sub-plot was used for gathering observations on this species. Data on *T. troglodytes* were collected in 1977–78 and on the *Phylloscopus* warblers in 1977–79. Detailed descriptions of the plots are given in Wesołowski (1983), Tomiałojć *et al.* (1984) and Piotrowska and Wesołowski (in press).

The period of field work each year (10 April–30 June) covered the whole laying period of *P. sibilatrix* but mostly the period of first broods in the remaining species. In 1978 observations were continued until the end of July.

Each year the males were mist-netted and individually marked. In the case of *P. sibilatrix* it was also possible to ring the females (for descriptions of catching methods see Wesołowski 1982).

Territorial males were followed and location of their consecutive song posts were plotted on large scale maps in order to delimit size of their territories. In the case of the warblers, play-backs of their songs were also used.

In order to obtain data on the mating and breeding success of territory owners, females and nests were searched for in all the territories. It was possible to find practically every nest in territories of the *Phylloscopus* warblers, but, despite much effort, the finding of all nests of *T. troglodytes* was not achieved. Therefore, additional visits were made to territories of the latter species in order to record the presence of newly fledged families (Wesołowski 1983).

RESULTS

Background information on the breeding biology of the species studied

A more detailed analysis of the breeding biology of these species is presented elsewhere (WESOŁOWSKI 1980, 1981a, 1981b, 1983, 1985, PIOTROWSKA and WESOŁOWSKI in press). Thus only a short summary of information relevant to the study of mating systems is given here. All species are small, insectivorous, migratory birds in which males occupy all-purpose territories in the

Table 1. Some life-history aspects of the species studied (following WESOŁOWSKI 1980, 1983, 1985, PIOTROWSKA and WESOŁOWSKI in press)

Specified are those features which, according to various authors (von HAARTMAN 1969, EMLEN and ORING 1977, CAREY and NOLAN 1979), could have an impact on the type of mating system

Tabela 1. Niektóre aspekty biologii badanych gatunków (według WESOŁOWSKI 1980, 1983, 1985, PIOTROWSKA i WESOŁOWSKI w druku)

Uwzględniono te cechy, które według różnych autorów (von HAARTMAN 1969, EMLEN i ORING 1977 CAREY i NOLAN 1979) mogą mieć wpływ na typ systemu kojarzenia

Feature — Cecha	*P. sibilatrix*	*P. collybita*	*T. troglodytes*
Length of singing period — Długość okresu śpiewu	*c.* 70 days dni	*c.* 95	110–120
Length of egg-laying period — Długość okresu składania jaj	*c.* 45	*c.* 55	*c.* 80
Nest type and location — Typ i umieszczenie gniazda	Domed, on the ground — Zamknięte, na ziemi	Domed, on the ground or low above it — Zamknięte, na ziemi	Domed, low above the ground — Zamknięte, nisko nad ziemią
Share of male in: Udział samca w:			
nest-building budowie gniazd	None Brak	None Brak	Builds external layer of nests — Buduje zewnętrzną warstwę gniazda
incubation inkubacji	None Brak	None Brak	None Brak
feeding young karmieniu piskląt	Substantial, roughly equal to that of female — Znaczny, odpowiadający udziałowi samicy	Little Wyjątkowy	Little Wyjątkowy
Sexual dimorphism Dymorfizm płciowy	Only in body size Tylko rozmiarów ciała	Only in body size Tylko rozmiarów ciała	Only in body size Tylko rozmiarów ciała

breeding period. The females come back from winter quarters later than the males, and pair-formation takes place on territory.

Although there are general similarities, the species differ in many respects, *e.g.* length of breeding period or participation of males in parental care (Table 1). They differ as well in types of preferred habitats — *T. troglodytes* and *P. collybita* settle in highest densities in the swampy ash-alder stands, whereas *P. sibilatrix* breeds in highest densities in the oak-hornbeam stands (Table 2).

Table 2. Mean densities (territories/10 ha) of *T. troglodytes*, *P. collybita* and *P. sibilatrix* in the habitats studied

Tabela 2. Przeciętne zagęszczenia *T. troglodytes*, *P. collybita* i *P. sibilatrix* w badanych siedliskach (zagęszczenia podano w terytoriach/10 ha)

Species Gatunek	Habitat type — Typ siedliska		Source Źródło
	Oak-hornbeam Grąd	Ash-alder Łęg	
T. troglodytes	1.7	4.3	Wesołowski (1983)
P. collybita	0.8	4.0	Piotrowska i Wesołowski (in press)
P. sibilatrix	7.0	3.9	Wesołowski (1980)

Polygyny

Polygyny occurred regularly in all the species studied (Tables 3 and 4). In spite of small number of cases recorded the polygyny in *T. troglodytes* and *P. collybita* cannot be treated as incidental because polygynists were observed in three out of four study years (Table 3, Wesołowski 1983).

Males were usually able to attract only two females simultaneously. Trigamy was observed only once in *P. collybita* and once in *P. sibilatrix* (Tables 3 and 4). Though males of *P. sibilatrix* were infrequently polyterritorial (Wesołowski 1980) in all recorded cases of polygyny, the nests of different females were built within the same territory.

The polygynous males of *P. collybita* and *T. troglodytes* were found in ash-alder stands (Table 3) whereas, all but one polygynous males of *P. sibilatrix* possessed territories in oak-hornbeam stands (Table 4). For each of those species the habitat in which polygyny occurred constituted its high-density habitat (*cf* Table 2).

Within the high-density habitats, however, the proportion of polygynous males varied in different years from zero to 40% (*P. sibilatrix* — plot C, 1978, Table 4). In some instances the presence of polygynous males was balanced by simultaneous occurrence of bachelors within the study plots, and the ratio of territory holders to nesting females was close to unity. More frequently, however, female skewed sex ratio occurred, up to 1.44 females/male being recorded (Table 4).

Table 3. Mating success of *T. troglodytes* and *P. collybita* males in different years and habitats

OH = oak-hornbeam habitat, AA = ash-alder habitat. Numbers shown refer to a maximum number of females breeding simultaneously in individual territories in the period of first broods. Only for *P. collybita* in 1978 are data for the first and second broods given

Tabela 3. Udatność kojarzenia samców *T. troglodytes* i *P. collybita* w różnych latach i siedliskach

OH = grąd, AA = łęg. Przedstawione wartości oznaczają maksymalną liczbę samic gnieżdżących się jednocześnie w poszczególnych terytoriach w okresie pierwszych lęgów. Tylko dla *P. collybita* w 1978 r. podano dane dla okresu pierwszych i drugich lęgów

Species Gatunek	Years Lata	Plot and habitat Powierzchnia i siedlisko	Number of males with: Liczba samców z: 0 1 2 3 females — samicami	% of polygynous males % poligynicznych samców	Males: females Samców: samic
T. troglodytes	1976–79	K — AA	3 21 5 —	17.2	1 : 1.07
	1977–78	C — OH	1 14 — —	0	1 : 0.93
P. collybita	1976	K — AA	1 5 1 —	14.3	1 : 1.0
	1977	K — AA	1 9 1 1	16.7	1 : 1.17
		C — OH	1 3 — —	0	1 : 0.75
	1978	K — AA —			
		I brood — lęg	1 7 2 —	20.0	1 : 1.10
		II brood — lęg	3 4 2 —	22.2	1 : 0.89
		C — OH —			
		I brood — lęg	2 3 — —	0	1 : 0.75
		II brood — lęg	3 1 — —	0	1 : 0.25
	1979	K — AA	1 10 — —	0	1 : 0.91
		C — OH	2 5 — —	0	1 : 0.71
Totally	1976–79	K — AA —			
		I brood — lęg	4 31 4 1	12.5	1 : 1.05
Łącznie	1977–79	C — OH —			
		I brood — lęg	5 11 — —	0	1 : 0.69

In spite of the yearly changes in proportion of males to females, the between-habitat differences remained constant, every year the males in the high-density habitat had mating success better or equal to that of the males in the low-density habitat (Table 3 and 4).

Polygynous males had slightly larger territories on average than monogamous and bachelor ones (Table 5) but only in the case of *P. sibilatrix* in plot K was the difference between mean values significant ($p < 0.001$, t-test, two-tailed). The range of territory sizes of individual polygynous males was fairly large, the smallest territories of polygynists were usually below the average size of the monogamous males territories (Table 5).

As shown by Wesołowski (1980), in the low-density (ash-alder) habitat *P. sibilatrix* used patches with different vegetation structure to a varying extent — the birds avoided areas with open canopy and very dense, tall herb

Table 4. Mating success of *P. sibilatrix* males in different years and habitats

Other explanations as in Table 3

Tabela 4. Udatność kojarzenia samców *P. sibilatrix* w różnych latach i siedliskach

Pozostałe objaśnienia jak w tabeli 3

Year Rok	Plot and habitat Powierzchnia i siedlisko	Number of males with: Liczba samców z: 0	1	2	3 females — samicami	% of polygynous males % poligynicznych samców	males: females Samców: samic
1976	K — AA	—	11	—	—	0	1 : 1.0
	K — OH	1	8	2	—	18.2	1 : 1.09
1977	K — AA	—	—	—	—	—	
	K — OH	2	6	1	—	11.1	1 : 0.89
	C — OH	3	17	3	—	13.0	1 : 1.0
1978	K — AA	1	7	1*	—	11.1	1 : 1.0
	K — OH	—	12	3	—	20.0	1 : 1.20
	C — OH	—	15	9	1	40.0	1 : 1.44
1979	K — AA	1	4	—	—	0	1 : 0.80
	K — OH	—	8	2	—	20.0	1 : 1.20
	C — OH	3	15	1	—	5.3	1 : 0.89
Totally Łącznie	K — AA	2	22	1	—	4.0	1 : 0.96
	K — OH	3	34	8	—	17.8	1 : 1.11
	C — OH	6	47	13	1	20.9	1 : 1.13

* Actually only one female built nest in this habitat. Territory of this male contained also a small patch of OH habitat and the second nest was placed there.

* Tylko jedna z samic zbudowała gniazdo w tym siedlisku. Terytorium tego samca zawierało również niewielki fragment grądowy, w którym to zbudowała gniazdo druga samica.

Table 5. Territory size, breeding success of males with different mating status and breeding success of their females in the high density habitats in the years in which polygyny was recorded

M — monogamous, P — polygynous, B — bachelor

Tabela 5. Wielkość terytoriów, udatność lęgów samców o różnym statusie i udatność lęgów ich samic w siedliskach o wysokim zagęszczeniu w latach, w których obserwowano poligynię

M — monogamiści, P — poligyniści, B — samce samotne

Species Gatunek	Plots and years Powierzchnie i lata	Male's status Status samca	No. of males Liczba samców	Territory size (ha) Wielkość terytorium (ha) $\bar{x}$	(Range) (Zakres)	No. of successful nests per Liczba pomyślnych lęgów na male samca	female samicę
T. trogl.	K — 1976,	M + B	14	2.20	(0.64–3.74)	0.58*	0.58
	1978, 1979	P	5	2.67	(1.85–4.02)	1.40	0.70
P. collyb.	K — 1976–	M + B	24	1.60	(0.41–2.95)	0.66*	0.66
	1978	P	5	1.72	(1.25–1.99)	1.20	0.54
P. sibil.	K — 1976–	M + B	17	0.60	(0.22–1.25)	0.33*	0.33
	1979	P	7	0.92	(0.64–1.13)	0.90	0.45
	C — 1978	M	10	0.86	(0.58–1.05)	0.09	0.09
		P	10	0.94	(0.62–1.74)	0.32	0.15

* Bachelors excluded.

* Z wyłączeniem samców samotnych.

vegetation. Application of the same set of vegetational variables, as used in the former analysis, for comparisons of vegetation structure in territories of monogamous and polygynous males in the high-density (oak-hornbeam) habitat revealed however, (Table 6), that the vegetation structure of these two samples of territories was almost identical. Thus, one could not explain variation of

Table 6. Vegetation structure in the territories of monogamous (N = 10) and polygynous (N = 10) males of *P. sibilatrix*. Plot C, 1978

Data on vegetation structure were collected in points uniformly distributed over territories. Depending on territory size the vegetation was sampled in 10–28 points (WESOŁOWSKI 1980). The values shown are means of mean values for individual territories. None of the differences was significant

Tabela 6. Struktura roślinności w terytoriach monogamicznych (N = 10) i poligynicznych (N = 10) samców *P. sibilatrix*. Powierzchnia C, 1978 r

Dane o strukturze roślinności zbierano w punktach rozmieszczonych równomierne w terytoriach. Zależnie od wielkości terytorium strukturę mierzono w 10–28 punktach (WESOŁOWSKI 1980). Pokazane wartości są wartościami przeciętnymi wyliczonymi ze średnich wartości parametrów w poszczególnych terytoriach. Żadna z różnic nie jest statystycznie istotna

Habitat parameter Cecha siedliska	Monogamous males Samce monogamiczne	Polygynous males Samce poligyniczne
Mean closure by the canopy and subcanopy layers Przeciętne pokrycie warstwy koron i podszytu	0.87	0.87
Mean coverage of herb layer Przeciętne pokrycie warstwy zielnej	0.52	0.47
Average height of herb layer (cm) Przeciętna wysokość warstwy zielnej (cm)	13	12

male mating success in the oak-hornbeam habitat in terms of structural differences among the territories. In the case of *T. troglodytes* and *P. collybita*, furthermore, it was impossible to predict, on the basis of the habitat structure in their territories, which male would attract two mates. Though the vegetation structure did not change among years (except of falling of a few trees), the position of bachelor and polygynous males territories did change — in all three species the same place could be occupied by a bachelor male in one year and by bigamist in the other — an example of such situation is shown in Fig. 1.

Due to low site-tenacity (WESOŁOWSKI 1980, 1983, PIOTROWSKA and WESOŁOWSKI in press) the observations of mating success of males in consecutive seasons are few — Table 7. Nevertheless, they show that the male's ability to attract females was not a fixed feature of an individual, the *P. sibilatrix* male bigamous in one year could fail to attract any mate the next, *e.g.* male 88 (Table 7). The data on the mating success of *P. collybita* males during period of first and second broods in 1978 (Table 3) illustrate this variability as well.

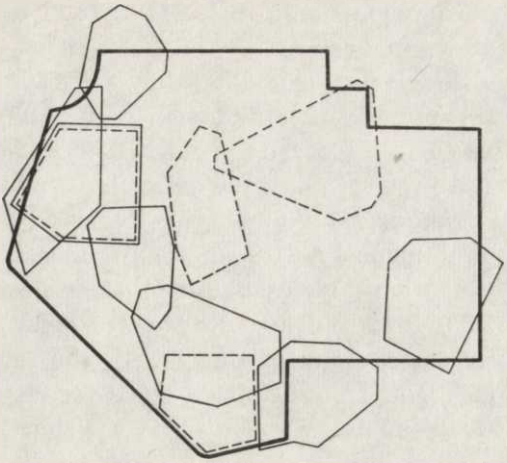

Fig. 1. Distribution of territories of polygynous (solid lines) and bachelor (dashed lines) males of *P. collybita* in the ash-alder habitat (plot K) (all years data combined)

Ryc. 1. Położenie terytoriów poligynicznych (linie ciągłe) i samotnych samców *P. collybita* w łęgu (pow. K) (naniesiono dane z wszystkich lat)

Table 7. Mating success of males returning to the study site in consecutive seasons

The success expressed as the maximum number of females breeding simultaneously within the male's territory. " — " male absent

Tabela 7. Udatność kojarzenia samców wracających w kolejnych sezonach

Udatność przedstawiona w postaci najwyższej liczby samic gnieżdżących się jednocześnie w terytorium samca. " — " samiec nieobecny

Species Gatunek	No. of the male Nr samca	Number of females in: Liczba samic w r.:			
		1976	1977	1978	1979
P. collybita	5	1	1	1	—
	33	1	2	—	—
	52	—	1	2*	1
P. sibilatrix	65	1	1	—	—
	88	—	—	2	0
	48	—	1	—**	—

* Bachelor in period of second broods (July).
W okresie drugich lęgów (lipiec) bez samicy.

** The male unsuccessfully attempted to establish territory.
Samiec bez powodzenia próbował zająć terytorium.

One of first brood bigamists failed to attract any mate during the period of second broods, while two other males which were monogamous during the first brood became bigamists during second broods. This occurred even though all these males occupied the same territories during the whole season.

Primary females of polygynists in both *Phylloscopus* species settled one-two days earlier on an average than the females of monogamous males, though in

neither case was the difference significant. If dates of egg-laying commencement in the earliest nests in every season were used as a point of reference (day one), than the average first-egg date was 4.9 days in primary *P. sibilatrix* females ($N = 18$) and 5.7 days in females ($N = 38$) mated with monogamous males ($p > 0.3$, KOLMOGOROV-SMIRNOV test). The polygynous males were not necessarily the first to mate, for example in plot C in 1978 the first polygynous male of *P. sibilatrix* acquired his primary mate later than the two monogamous ones, simultaneously with another monogamous male; similarly in *P. collybita* – the bigamous males obtained their first females later than one monogamous male in 1977 and, in 1978, one of bigamous males attracted his primary female very late, simultaneously with the settling of a female in the territory of the last monogamous male. The time-lag between settlement of primary and secondary females was often very short, 50% of secondary *P. sibilatrix* females settled only 0–4 days later than the primary ones, and almost 82% of them built their nests within 10 days following the start of building by the primary ones. Similarly, in *P. collybita* 50% of secondary females settled within 0–4 days following the primary ones. The nests of primary and secondary females, especially in *P. sibilatrix* were frequently close to each other, at a distance of 20–25 m. The females could easily see and hear each other but no apparent conflicts among them, at least at later stages of breeding cycle, were visible.

Comparisons of breeding success of monogamous and polygynous males (Table 5) revealed that the success of the latter was two to three times better than the former.

Due to many cases of simultaneous or almost simultaneous settlement of females (*cf* above) it has been impossible to make a reasonable division of females into primary and secondary ones. Thus, only mean nesting success of females mated to polygynous males was calculated (Table 5). The success of females mated to polygynous males was equal to (*T. troglodytes*, *P. collybita*) or even higher (*P. sibilatrix*) than the success of females mated to monogamous males (Table 5). Though these differences are not statistically significant (KOLMOGOROV-SMIRNOV test) they were consistent between years and areas; in *P. sibilatrix* in six out of seven plots and years compared, the success of females mated to polygynous males was better than that of females mated to monogamous males. Variation of breeding success was brought about mainly by predation, no starvation was recorded (WESOŁOWSKI 1983, 1985, PIOTROWSKA and WESOŁOWSKI in press).

DISCUSSION

Polygyny has been found by earlier workers in each of the three species. It is a common phenomenon in *T. troglodytes* (KLUIJVER *et al.* 1940, GARSON 1980, LOVATY 1985) and *P. sibilatrix* (papers reviewed in von HAARTMAN 1969

and FOUARGE 1968, HERMAN 1971, OVTCHINNIKOVA and FIRSOVA 1971, OVTCHINNIKOVA 1973, TEMRIN 1984 and personal com.). In *P. collybita*, however, all proved and suspected cases of polygyny reported so far (review in SCHÖNFELD 1978) are fewer than their number recorded in this study (*cf* Table 3). Similarly in a parallel study carried out in a managed part of the Białowieża Forest (PIOTROWSKA and WESOŁOWSKI in press) only one case of bigamy in over 120 territories under observation was recorded. This rare occurrence of polygyny in *P. collybita* and much more frequent appearance of it in *P. sibilatrix* is at variance with some theoretical expectations (CROOK 1965, VERNER and WILLSON 1966, EMLEN and ORING 1977, CAREY and NOLAN 1979). Indeed, according to the theory, one would expect to find many cases of polygyny in *P. collybita* in which the male parental care is strongly reduced and breeding and singing periods are very long (*cf* Table 1); *P. sibilatrix*, in contrast has a short breeding season and males of that species accompany incubating females and regularly feed nestlings, therefore they should be monogamous or infrequently polygynous. The latter case shows that male emancipation from parental duties or long periods in which fertilizable females are available are not indispensable preconditions for polygyny to occur.

Mating system of all three species is best described as facultative polygyny (WESOŁOWSKI 1981c) of the resource defence type (EMLEN and ORING 1977). In such a system the males defend territories which contain attributes attractive to females; majority of males are monogamous, some males are bigamous (exceptionally trigamous) while others remain unmated. There is a strong between-year and-habitat variability in the proportion of polygynous males to monogamous and bachelor ones.

What are the possible routes which could lead to appearance of facultative polygyny? I attempt to answer this question below, but before plunging into this problem I should like to consider some questions connected with paternity of broods.

Paternity issues

A basic assumption in my analysis is that territory owners sired the young born in their territories. This, however, need not always be true, as GLADSTONE (1979), FORD (1983), MOCK (1983) and MC KINNEY *et al.* (in press) in a series of recent reviews raised a question of mixed brood paternity in birds with "strictly" monogamous pair bonds. Evidence of extra-pair copulations, mate guarding and intrusions of neighbours into territories with fertilizable females has been found in a wide array of monogamous species, which suggests (but *cf* FITCH and SHUGART 1984) that assessment of paternity may be quite a serious problem. Mixed brood paternity and extra-pair copulations were also recorded in polygynous species: *Agelaius phoeniceus* (ROBERTS and KENNELLY 1980, BRAY *et al.* 1975) and *Ficedula hypoleuca* (BJÖRKLUND and WESTMAN 1983, ALATALO *et al.* 1984).

There is some indication that confidence of paternity may be a problem also in the species dealt with in this study. Extra-pair copulations have been recorded in *P. sibilatrix* (Herman 1971, the females accepted strange males in spite of their mates attempts to drive the intruders away). Brood adoption by males (Wesołowski 1981a) and feeding young by two males simultaneously (Fouarge 1968, Tiedemann 1972, Wesołowski 1981a) recorded in this species could also be suggestive of mixed paternity (*cf* Davies 1985). Single cases of simultaneous feeding of young by two males were observed as well in *T. troglodytes* (Armstrong and Whitehouse 1977). In both *Phylloscopus* species the males closely followed females while they were building nests (Homann 1960, Wesołowski 1980, Piotrowska and Wesołowski in press), probably indicating that they were guarding mates during the receptive period. On the other hand, intrusions by territory owners into territories of other males, especially during pair-formation and nest building, were frequent in all three species (Armstrong 1955, Mühlenberg 1964, Aschenbrenner 1966, Herman 1971, Wesołowski 1980, Piotrowska and Wesołowski in press), and in *T. troglodytes* Wesołowski (1981b) recorded the presence of males that were non-territorial, yet physiologically capable of reproduction.

Taking into account all the above, it is possible that also in the three species studied in the Białowieża National Park not all eggs laid in territories were fertilized by the territory owners. This, however, would influence further arguments only if polygynous males were loosing relatively more from eventual "cuckoldry" than the monogamous ones. Unfortunately, the assessment of this problem is impossible with the data at hand.

Models for the evolution of polygyny based on female choice

Polygyny threshold models

Verner (1964), Verner and Willson (1966) and Orians (1969) proposed an explanation of polygyny evolution based on female choice. When resources are patchily distributed the differences in the quality of male territories might be great enough that females can achieve higher fitness mating with already mated males possessing rich territories than with unmated males possessing low-quality territories despite the prospect of losing some, or all of the male's assistance in provisioning their young. The difference in territory quality sufficient for this to occur has been termed "polygyny threshold".

These first papers were followed by a flux of publications proposing more elaborated versions of the model (*e.g.* Altmann *et al.* 1977, Lenington 1980, Wittenberger 1981, Garson *et al.* 1981, Oring 1982, Vehrencamp and Bradbury 1984). The authors often express quite contradictory opinions on what does and what does not constitute a proper test of the polygyny threshold model, and, in consequence "the resulting literature is a morass of conflicting claims and counter-claims" — Vehrencamp and Bradbury (1984).

I am not going to add to this theoretical confusion, instead I would like to concentrate on some methodological problems connected with field data gathering which have so far escaped attention of theoreticians.

Following the first formulations of the polygyny threshold model (Verner 1964, Orians 1969) scores of other students repeated the notion, which by now had become almost axiomatic, that females choose their mates on the basis of quality of their territories. The statement that females base their choice on territory quality is an assumption which should be throughly tested. To show that females evaluate territory quality, one should demonstrate that, while making decisions, the birds know positions of territory borders of their would-be mates and evaluate quality of areas within these borders. Strangely enough I know of no study aimed at checking this possibility.

Data which could shed some light on this problem are few. Settling females of *P. sibilatrix* do not respect territory boundaries of their males, not infrequently they choose their nest-sites outside their males territories and the males must enlarge territories in order to accomodate nests in them. This is a fairly widespread phenomenon, as it was recorded in Belgium (Herman 1971), Soviet Union (Ovtchinnikova and Firsova 1971) and in the Białowieża Forest (Wesołowski 1980). Also in *P. collybita* and *P. trochilus* some instances of choosing nest-sites by females outside territories of their males were observed (Lawn 1982, Piotrowska and Wesołowski in press). In *T. troglodytes* the males provide females with nests, and thus the females cannot choose to nest outside male's territory without changing the male as well. Yet even in this species the breeding females do not respect territory borders and frequently enter into territories of other males (Armstrong 1955).

Similarly in *Prunella modularis* "the females are not constrained in their movements by male territory boundaries when they set up their ranges in spring" — Davies and Lundberg (1985).

Thus, at least for the species listed above, one cannot speak about females choosing territories. The females probably choose some habitat patches but not the territories themselves.

If the females do not choose territories then measurements of territory quality need not necessarily be valid estimates of quality of areas chosen by females. One should rather measure habitat quality of the area utilized by females. Another, less preferable solution, could be an evaluation of habitat quality in some arbitrarily chosen areas, for example, within a fixed radius from nests, or as Searcy (1979) and Yasukawa (1981) did, in arbitrarily selected habitat patches.

All formulations of the polygyny threshold models include the notion of female fitness — the females should make their choices so as to maximize their fitness. There is a serious methodological difficulty in testing this assumption. The settling females must make their decisions relying on their estimates of expected fitness gains. On the other hand, in the field we are able to measure

only the realized fitness gains. As the expected gains may be achieved or not, the ranking of females according to these two measures may give quite different results. For example, in areas with heavy nesting losses due to predation, like the Białowieża Forest (Wesołowski 1983, 1985, Piotrowska and Wesołowski in press) the majority of females fail to rear offspring altogether. Thus, using production of young as a measure of the realized fitness we should give an identical rank — no young — to over 50% of females. It is almost impossible to imagine that any of those females, while settling, was expecting that she would produce no young at all.

Most proposals of the polygyny threshold model testing include a postulate to rank the quality of male territories and to compare these ranks with ranking

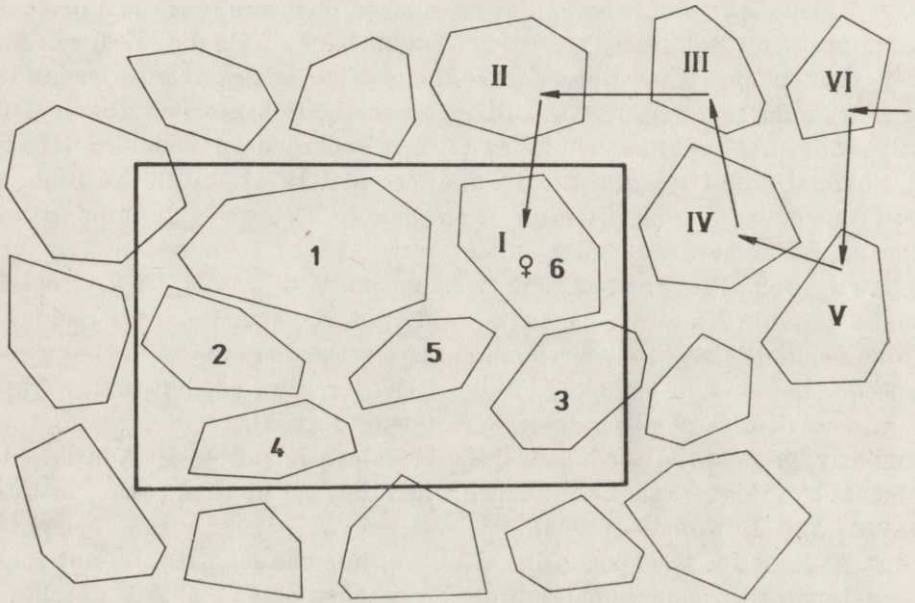

Fig. 2. Hypothetical example of territory distribution within a study area and its surroundings

Ranking of territory quality by an observer is marked with Arabic numerals. Consecutive movements of a prospecting female are marked with arrows and her ranking of territories with Roman numerals. Though the observer and the females use exactly the same criteria to evaluate territory quality, as they assess only partially overlapping sets of territories, the female gives the highest rank to and settle in a territory ranked lowest by the observer. This illustrates a situation which may be very frequent in the real world and can lead to erroneous conclusions, yet this methodological problem has not been recognized in earlier studies of female choice

Ryc. 2. Hipotetyczny obraz rozmieszczenia terytoriów na powierzchni próbnej i w jej okolicy

Wyniki oceny jakości terytoriów dokonanej przez badacza oznaczono cyframi arabskimi. Kolejne przemieszczenia dokonującej wyboru samicy zaznaczono strzałkami, a jej oceny jakości terytoriów cyframi rzymskimi. Mimo iż obserwator i samica używali dokładnie tych samych kryteriów dla oceny jakości terytoriów, to jednak ze względu na to, że próbki ocenianych terytoriów pokrywały się tylko w niewielkim stopniu, samica oceniła najwyżej i osiedliła się w terytorium, które zostało ocenione jako najgorsze przez badacza. Przykład ten ilustruje sytuację, z którą można się często spotkać w rzeczywistości, a która może prowadzić do błędnych wniosków. Ten problem metodologiczny nie został jak dotąd dostrzeżony w badaniach wyboru dokonywanego przez samice

of territories by the settling order of females and/or final harem size in the territories. Let us assume for a moment that both an observer and settling females use exactly the same criteria to assess territory quality and that the birds really choose territories (*cf* above). In such a situation the ranking of territories by the females and the observer should agree. This, however, only under condition that both sides estimated quality of the identical set of territories. If the subsets of territories sampled differ, the rankings by the females and the observer may disagree (Fig. 2) and one may arrive at completely wrong conclusions.

This constitutes a serious problem in field studies. Usually one has to concentrate on observations of a score of males being members of a much larger local population. How to constrain females to choose mates only from among our sample of males? How to assert that every female will check quality of all territories within our study area before settling? These are difficult methodological questions, but without solving them there is little hope for any real progress in studying territory quality/female choice problems.

Taking into account the methodological problems discussed above, as well as lack of agreement among theoreticians on what should constitute a proper test of the polygyny threshold model (*cf* p. 285), it seems reasonable to conclude that at present it is impossible to collect data with which one could unequivocally test the model.

Male genetic quality model

Even the first proponents of the polygyny threshold model (Verner 1964, Orians 1969) proposed that females should base their choices not only on territory quality but also on male quality. Wittenberger (1976) included both habitat and male quality in his concept of "quality of the breeding situation". However, the majority of workers concentrated only on attempts to correlate female distribution and territory quality and did not treat male quality as a separate variable. Only after finding that the nesting success of secondary females was much lower than that of females mated to monogamous males, was the male genetic quality recalled in order to rescue the hypothesis of adaptive female choice (Weatherhead and Robertson 1979). The authors argued that the females choosing secondary status, though losing out in the short term, may benefit in the long term by producing "sexy sons", which in turn, by being more attractive to females will produce more grandchildren, *i.e.* they used the same argument as used by Fisher (1930) for the explanation of the evolution of epigamic traits. Weatherhead and Roberston (1979) assumed that the mating status of males is highly heritable and sons inherit to large extent their fathers ability to attract females. Though the authors did not mention this, but from their argument it logically follows that if the male mating status was strongly genetically controlled, then one would expect a mating status

of the "sexy" individuals to be always higher or equal to that of other males in a population.

The observations collected in the Białowieża National Park do not confirm this prediction. They show that the relative mating status of males could be highly variable, it could change between years and even between consecutive broods in the same season (*cf* Table 7 with Table 3 and 4). Similar variability was also found in *Phylloscopus trochilus* (LAWN 1982), *Acrocephalus arundinaceus* (PELTZER 1972), *Agelaius phoeniceus* (SEARCY 1979, YASUKAWA 1981), *Prunella modularis* (DAVIES and LUNDBERG 1984) and *Passerina cyanea* (CAREY and NOLAN 1979).

The variability of mating success found in individual males speaks against the possibility of high heritability of male "sexiness" (life-time mating success of a male which is bachelor one year, monogamous the next and bigamous the third year equals that of a male mating monogamously three successive years). Thus, it may well be that, at least in the above mentioned species, females when accepting secondary status, cannot count on substantial long-term genetical benefits. As a result, they should rather settle so as to maximize their direct fitness, *i.e.* their life-time production of young.

Broadening a field of view: beyond the limits of females choosing mates

The hypotheses on the polygyny evolution discussed so far attempted to explain the phenomenon considering only the female choice of mates and territories. Does this theoretical framework suffice to explain the evolution of polygyny? Do actually all cases of the resource defence polygyny depend only on variation in male and/or territory quality? I do not think that one can answer affirmatively these questions. My doubts stem from two reasons, which will be discussed in turn:

1. mate choice is probably only the last step in a series of decisions leading to female settlement, decisions made at earlier steps may influence the very occurrence, as well as the extent of polygyny
2. female choice models do not leave any role for male activity, the males are treated as passive objects to be chosen by females.

Hierarchy of decisions to be made by the females

If a female of migratory species selects where to breed she has to decide at least three different levels:

1. when to stop migration (this will demarcate general region of settling)
2. which habitat within this region to settle in
3. what patch within the habitat to choose and which male to mate with.

As it is clearly seen from this specification the male/"territory" quality evaluations become important only at the third level of resolution. Yet the

factors influencing decisions at the first and second level may be much more important, as choice made at these levels will determine whether the females will at all check male/"territory" quality within a given habitat.

Factors responsible for termination of bird migration of females are still poorly understood (GWINNER and CZESCHLIK 1978). In site-tenacious species returning to their former breeding places, a proximate factor inducing females to stop migration may be recognition of their target area.

In other species, which are not site-tenacious, distances covered during migration and places of settlement may vary, being strongly dependent on weather conditions en route. In warm springs the birds fly further and settle more to the North than in cold ones — so called phenomenon of "prolonged migration" (SVÄRDSON 1949). As males migrate earlier than females, the sexes may encounter different weather conditions along their routes. This in turn may result in non-uniform distribution of sexes within a breeding range and locally skewed sex ratios. This mechanism seems responsible for year-to-year variation in numbers and variable sex ratios in the Białowieża *P. sibilatrix* (WESOŁOWSKI 1980). Indeed in order to account for this variation with habitat/male quality arguments one would have to assume that, for example in plot C in 1978, the male quality and/or habitat quality were severalfold higher than in 1979 (40 and 5 % of polygynous *P. sibilatrix* males respectively — *cf* Table 4). Considering the fact that habitat structure did not change between these years, that territory sizes were similar and that the main food resource — leaf-eating caterpillars were about four times more abundant in 1979, when polygyny was rare (WESOŁOWSKI 1980, TOMIAŁOJĆ *et al.* 1984), these arguments are not tenable, at least in their part dealing with "territory" quality.

After terminating migration the females must choose in which habitat to breed. To a large extent this has not been recognized by students of the evolution of polygyny (usually papers on this subject contain no references to the main theoretical papers on habitat selection, such as for example HILDÉN 1965 or FRETWELL and LUCAS 1969). Habitat quality has been usually treated as a subset of a very vague "territory quality" category. Such an approach tends to obscure the possibility that females may use different criteria to evaluate habitats and "territories"/males (*cf* also LENINGTON 1983). A bird selecting between settling in, for example, deciduous or coniferous forest, or between marshland and upland vegetation needs only to know what are the basic suitabilities (FRETWELL and LUCAS 1969) of these habitats, *i.e.* what fitness it can expect to achieve by settling in one or the other (this may be highly predictable, as ranking order of female productivity in different habitats tend to remain stable between years — *e.g.* TOMIAŁOJĆ 1980, WESOŁOWSKI 1985, PIOTROWSKA and WESOŁOWSKI in press); and be able to recognize the habitats correctly. This is enough to make a correct choice. The bird needs not know anything about quality of territories and males except that there are some present.

It seems that choices made at the habitat level of resolution determine to a large extent the numbers of birds settling in different habitats and mate/"territory" evaluation decides only on non-uniform distribution of females within the habitats.

Data collected in the Białowieża Forest (*cf* p. 277) agree well with such an explanation. In all three species the polygyny occurred (almost without exception) only in one type of habitat. In every case it was the habitat in which breeding densities were the highest.

Summing up, it seems that full understanding of factors leading to polygyny via female choice would demand studies of much wider spectrum of female decisions than it has usually been done.

Role of males in the evolution of polygyny

The female choice models discussed above treat males as passive entities from among which the females can choose. This view seems far too simplified. Though it is true that the females choose the males with which they will mate, but the models overlook that in a territorial system, it is the inter-male competition that decides which males enter the pool of candidates from which the females would make choice. Even the "sexiest" male, mating with whom would be very advantageous for females, has only a meagre chance to pass on his genes if he fails to establish a territory. Hence, in order to propose a complete explanation for the resource defence polygyny evolution one has to consider the males' role as well.

If we denote the maximum fitness gain an animal can expect to achieve from mating with a single partner with "S", then both the monogamous male and his female can expect to achieve "S". When a male mates with two females simultaneously — he can maximally expect to double his gains, *i.e.* to achieve 2 "S", but expectations of each of his females remain the same, *i.e.* — "S". Thus, for the females, the polygyny of their mates may be at best neutral (Altman *et al.* 1977 proposed that fitness of females might sometimes increase, but as no such case has been found so far, it is not considered here). Bigamy will be advantageous for males also when their expected gains will lay anywhere below 2 "S" but above "S". However, for the females any value below 2 "S" will be disadvantageous, as in such situation the fitness of one or both females has to be lowered. This creates a conflict of interest between the sexes. There is a built-in asymmetry in this conflict as males have very much to gain from being polygynous, the females, on the other hand, have (in the best case) nothing to gain from their mates being polygynous or (more probably) something to loose. If, however, eventual fitness losses in females were not great enough to create counter-selection pressures strong enough to neutralize selection in favor of polygyny in males, then one would expect polygyny to appear even if it were harmful for females. Furthermore one would expect

to find in males some ways of manipulating the females to accept secondary status.

In the resource defence polygyny the males attempt to control access to females indirectly, by defending territories in resource-rich areas (EMLEN and ORING 1977). MCLAREN (1972) argued that acquisition of multiple mates is the function of breeding territoriality in birds. He proposed that if some males were able to hold "superterritories", to control areas containing substantially more resources than needed for supporting a single mate and her progeny, than they could substantially increase their chances to obtain additional mates.

The majority of reviews (*e.g.* VERNER 1964, ORIANS 1969, EMLEN and ORING 1977) assume that heterogeneity of habitat is an indispensable prerequisite for unequal sharing of resources by males and monopolization of habitats by them. Though it seems true that the monopolizability of areas with uniformly distributed resources is more difficult than if they are spatially clumped, but it is not completely impossible (Fig. 3). In such circumstances, however, the only option available to males attempting to monopolize more resources is to increase the size of their territories. Larger territories may be advantageous from another reason as well. As shown earlier (*cf* p. 285) the prospecting females are not constrained in their movements by territory borders, yet it is much more probable that all displacements of the females would be accomplished within large than small territory.

From these arguments it follows that territory size should be an important variable, that males with larger territories should attract more females. This is only partially confirmed by my data. Though average territory size of polygynists was slightly larger than that of monogamous ones, in only one case was the difference significant (*cf* p. 278). A positive correlation between territory size and mating success was also found in some other species (VERNER 1964, ZIMMERMAN 1966, DAVIES and LUNDBERG 1984).

In heterogeneous habitats however, the males may increase amount of controlled resources not only by establishing larger territories but also by attempting to control areas with highest densities of resources. In such circumstances territory size alone may be a poor predictor of male success, as equally sized territories may substantially differ in quality (Fig. 3B) and, in extreme cases, smaller territories may even contain more resources than the larger ones. The situation observed in *T. troglodytes* and *P. collybita* in the Białowieża National Park illustrates the latter possibility quite neatly. Though the males in the oak-hornbeam habitat there possessed two-three times larger territories than the males in the swampy ash-alder forest, yet they often failed to get any mate, while the males in the latter habitat managed to attract multiple mates (*cf* Table 5 and WESOŁOWSKI 1983, PIOTROWSKA and WESOŁOWSKI in press).

An almost inevitable consequence of male attempts to control access to females and unequal sharing of resources would be prevention of some males

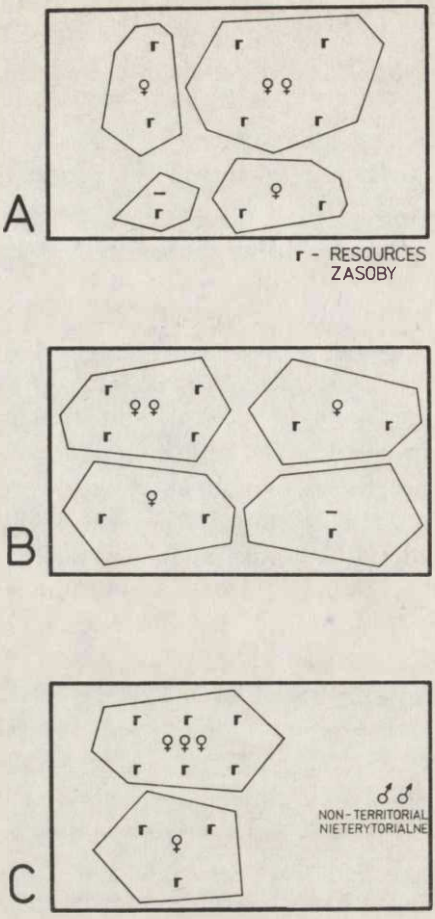

Fig. 3. Idealized diagrams showing how differences in resource distribution and male resource holding potential (PARKER 1974) may affect monopolization of resources by males and lead to polygyny in a population

Total amount of resources (denoted by "r"), number of females and number of males attempting to breed are the same in all versions of the Figure. In every case the females are distributed so that each has equal access to resources (ideal-free distribution type of FRETWELL and LUCAS 1969). A — when resources are uniformly distributed, the only chance of a male to get two mates is to increase substantially the area occupied by his territory; B — moderate clumping of resources facilitates their monopolization, some males can increase the amount of resources controlled without establishing unusually large territories; C — extreme clumping of resources enables a fraction of males to monopolize all the resources and leads to an excess of females in the reproducing part of a population. In the example shown there are two nesting females per one territorial male

Ryc. 3. Zidealizowany diagram pokazujący, w jaki sposób różnice rozmieszczenia zasobów i różnice zdolności utrzymywania zasobów (RHP — PARKER 1974) przez samce mogą wpływać na monopolizację zasobów przez samce i prowadzić do wystąpienia poligynii w populacji

Łączna ilość zasobów (zaznaczonych literami "r") oraz liczba samców i liczba samic próbujących się osiedlić jest taka sama na wszystkich wersjach ryciny. W każdym przypadku samice są rozmieszczone w ten sposób, że każda z nich ma jednakowy dostęp do zasobów (idealnie niezależny typ rozmieszczenia w modelu FRETWELLA i LUCASA 1969). A — gdy zasoby są równomiernie rozmieszczone, jedyną możliwością uzyskania przez samca dwóch samic jest znaczne zwiększenie obszaru zajmowanego przez niego terytorium; B — umiarkowane skupienie zasobów ułatwia ich zawładnięcie, niektórym samcom udaje się zwiększyć ilość posiadanych zasobów bez konieczności posiadania szczególnie dużych terytoriów; C — ekstremalne skupienie zasobów umożliwia ich opanowanie przez część samców i prowadzi do powstania nadwyżki samic w rozmnażającej się frakcji populacji. W podanym tu przykładzie na jednego terytorialnego samca przypadają dwie samice

from occupying territories, depending on numbers, either in the best (density level II in model of BROWN 1969) or in all habitats (density level III in BROWN 1969). In the latter case some males would be excluded from breeding in a local population. They might, however, emigrate and attempt to settle elsewhere or stay within the population as the nonterritorial floaters (Fig. 3C and 4).

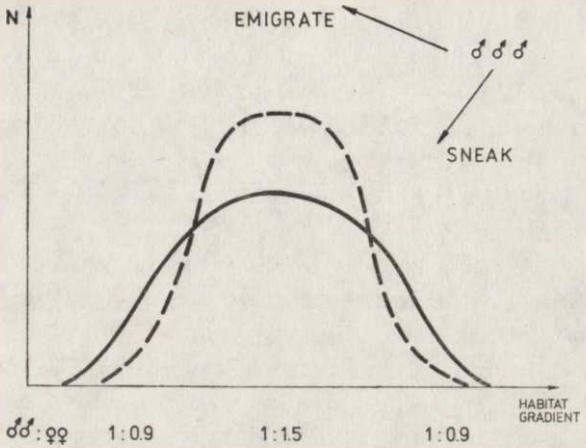

Fig. 4. A model of male (solid line) and female (dashed line) distribution over a gradient of habitats

The males are distributed according to the "ideal dominance" model (FRETWELL and LUCAS 1969), their numbers in all habitats are limited by the territorial behaviour, some males are deprived of the chance to get territories – *i.e.* density level III in the model of BROWN (1969). Non-territorial males may stay as "sneakers" or emigrate. All females breed, their distribution approximates the "ideal free" model of FRETWELL and LUCAS (1969). Because of the prevention of settlement of a fraction of males by territory holding birds, the sex ratio in the high-density habitats are female skewed, some males in these habitats acquire multiple matings

Fig. 4. Model rozkładu liczebności samców (linia ciągła) i samic (linia przerywana) w gradiencie siedlisk (habitat gradient)

Samce rozmieszczają się zgodnie z idealnym rozkładem dominacyjnym (FRETWELL i LUCAS 1969), ich liczebność we wszystkich siedliskach jest ograniczona przez zachowanie terytorialne, niektóre z nich są pozbawione możliwości zajęcia terytorium – odpowiada to III poziomowi liczebności w modelu BROWNA (1969). Ptaki nieterytorialne mogą pozostawać na miejscu czekając „na okazję" (sneak) lub emigrować (emigrate). Rozmieszczenie samic zbliżone jest do rozkładu idealnie niezależnego (FRETWELL i LUCAS 1969), wszystkie samice przystępują do rozrodu. Ze względu na uniemożliwienie przez właścicieli terytoriów osiedlenia się części samców w siedliskach o najwyższym zagęszczeniu występuje tam nadmiar samic. Powoduje to, że niektórym samcom w tych siedliskach udaje się uzyskać więcej niż jedną samicę

The males excluding others from establishing territories in a habitat would receive double gains, as they would not only control more resources but, by not allowing other males to settle, they would decrease the number of candidates available for prospecting females, which in turn would increase their personal chances of being chosen by the females. It should be stressed here that these arguments apply also to monogamous species, as in birds, due to higher female mortality, the males usually outnumber females (PAYEVSKY 1985). In such a situation a male has to exclude some other males from possessing territories in order to assure himself a good chance of getting even a single mate.

The existence of non-breeding males excluded from reproduction by the behaviour of territory holders or at least density limitation by territorial behaviour in optimal habitats was demonstrated in a great variety of species (review in Brown 1969 and Harris 1970, Zwickel 1972, Knapton and Krebs 1974, Krebs 1977, Smith 1978, Lewis and Zwickel 1980, Hannon 1983, Village 1983, Wesołowski *et al.* 1987). By experimental removal of males I was able to show that in the Białowieża National Park, the numbers of settling *P. sibilatrix* males in the high-density habitat was limited by territorial behaviour (Wesołowski 1980) and that a surplus of non-territorial, physiologically capable of reproduction *T. troglodytes* males occurred in the low-density habitat (Wesołowski 1981b).

Fretwell and Lucas (1969) proposed two models of habitat distribution of birds:

— "ideal free" — according to which birds have free choice of habitats and can always settle in the best habitat at any given time

— "ideal dominance" — according to which the birds are not allowed to settle in best habitats due to aggressive behaviour of earlier occupants.

As follows from the papers cited above, in a great variety of species the male distribution is clearly of the "ideal dominance type". Females, however, are as a rule much less aggressive than the males. Thus it seems reasonable to assume that their distribution should be (in relation to the males) more of "ideal free" type. What might be the consequences of these differences in modes of habitat distribution between the sexes for the occurrence of polygyny? A possible outcome of such discrepancies is shown in a simple graphical model — Fig. 4. Although the sex ratio of birds surviving till the breeding season was, in the example shown in the Figure, close to unity, due to prevention of some males from establishing territories altogether and preventing still more males from holding territories in habitats most attractive to females, the males in the best habitats have succeeded in creating of locally skewed sex ratios, which in turn enabled some males to attract multiple mates, and forced some females to accept secondary status, if they wanted to breed in the preferred habitats.

I would like to propose here that the situation illustrated by the model (Fig. 4) should commonly occur in the resource defence polygyny systems, and in habitats in which polygyny does occur we should be able to observe an excess of females. My proposal that the skewing of sex ratios is an important factor leading to polygyny seems completely contradictory to the current paradigm, according to which "skewed sex ratios may cause isolated instances of polygyny in normally monogamous species, but they are not responsible for the regular occurrence of polygyny in any species" — Wittenberger (1981). Unfortunately it is usually not specified what is meant by sex ratio. If it is the sex ratio of males to females at fledging or ratio of males to females surviving till the beginning of the breeding season, then there is no conflict between the paradigm and my proposal (*cf* above). Only if by "equal sex ratio"

it is meant that the ratio of territory holding males to breeding females in habitats in which polygyny occurs is equal, does a real contradiction with my arguments emerge.

I proposed (WESOŁOWSKI 1981c) to use the latter sex ratio as a measure of the extent to which males in different populations managed to monopolize access to mates. It could also serve as an approximate measure of intensity of intrasexual selection, competition among males. In the species studied in the Białowieża Forest, the sex ratio in the habitats in which polygyny occurred was usually female skewed, but even in the extreme case there were no more than 1.44 females/male (*cf* Table 3 and 4), *i.e.* fewer than 30 % of males were prevented from breeding in the best habitats.

In some, highly polygynous species, the sex ratios in breeding populations are much more strongly female skewed, in *Agelaius phoeniceus* they can reach even 6.8 females/male (*cf* SEARCY 1979 — Fig. 7). This means that 15 % of males monopolize all matings and prevent somehow the remaining 85 % of males from breeding.

The differences in monopolization level between the species studied in the Białowieża Forest (only small fraction of males becoming bigamists) and *Agelaius phoeniceus* (almost all territory holders polygynous, the most successful ones attracting up to 15 females — SEARCY 1979) reflect the disparities in environmental potential for polygyny. (EMLEN and ORING 1977), first of all in the extent of habitable environments. The three species studied in the Białowieża National Park live in a woodland forming a very large (over 1000 sq km) patch of habitats in relation to the male ability to control space (measured in hectares). *Agelaius phoeniceus*, on the other hand, breeds in marshlands which usually occur only locally, and areas covered with emergent vegetation in which females build their nests form most often discrete patches within the marshes. These patches are much smaller in relation to males capacity of controlling space than in the previous case. It enables a small fraction of *Agelaius phoeniceus* males to control all available habitats and has led to the evolution of extreme forms of polygyny.

WITTENBERGER (1976, 1979) argued that in species with dispersed breeding, like for example *T. troglodytes*, and in species with clumped resources, like for example *Agelaius phoeniceus*, the polygyny evolved following two separate routes. He suggested that in the former group all males could acquire territories but not all could attract mates and that the polygyny in this group has evolved via female choice of mates. For species with clumped nesting he proposed that some males could not settle due to aggressive behaviour of others, which created a situation in which some females had to accept secondary status. This differentiation is not confirmed by the existing data. As it was shown earlier (*cf* p. 294) the exclusion of males from holding territories by aggressive behaviour is commonplace in species with a dispersed type of breeding. Thus, there is no qualitative difference between these two groups. In both cases

males attempt to control access to nesting areas of females. The existing difference is only one of degree. It stems from the fact that when resources are clumped the birds have a much easier task and can prevent more males from possessing territories than if the resources are dispersed. If environmental conditions in the species with dispersed breeding changed so as to facilitate monopolization of resources, then the frequency of polygyny would rise. Data on *T. troglodytes* give some support to this idea. In the Białowieża Forest about 20% of males in the ash-alder habitat are bigamists (*cf* Table 3), whereas in the best habitats in England up to 50% of males are polygynous, and they can get up to three-four females simultaneously (Armstrong 1955, Garson 1978). This in spite of the English males having three-four times smaller territories than the Białowieża ones (Wesołowski 1983). The preferred nesting habitats of *T. troglodytes* in England — woodlands — are relatively more clumped, due to heavy deforestation of the British Isles (Wesołowski 1983). Hence they are easier to monopolize by males.

There is yet another difference between these two populations which might explain higher polygyny rates in England, *i.e.* much higher total population size there. Even if the total amount of habitats did not change, simply an increase in numbers would facilitate the appearance of polygyny (Verner 1964, Brown 1975). This is the necessary result if, as suggested above, habitat distribution of males and females are due to different mechanisms. As resistance of males to, increasing with population size, pressure of would-be settlers is much stronger than that of females, this would result in much slower increase of male than female density, which in turn would increase the skew of the sex ratio above the level possible at lower numbers.

So far in this chapter I have argued that the inter-male competition, ability of territory owners to prevent some males from settling in habitats attractive to females was the important force underlying the resource defence polygyny evolution. From these considerations it follows that we should not expect this type of polygyny in case when resources are not economically defendable (Brown 1964) and/or when the number of birds is so low that all of them can settle in the most attractive habitat (Brown 1975).

What could a male to do to improve his chances of attracting mates relative to other males in such a situation? The only option left to him is to pretend to be more than a single male, to show himself to prospecting females in several different places. This solution is found in several species, males of which practice so called "polyterritoriality", *e.g. Ficedula hypoleuca*, *Sylvia communis*, *Oenanthe oenanthe* (von Haartman 1969). The polyterritorial system also enables males to hide their marital status, as clearly demonstrated in *Ficedula hypoleuca* by Alatalo *et al.* (1981, 1982, 1984). In *P. sibilatrix* the male tactics depend on bird densities. In the Białowieża National Park, where the species was, as a rule, very numerous (Wesołowski 1980, Tomiałojć *et al.* 1984), the males attempted to prevent others from breeding and monoterritorial

polygyny occurred (*cf* p. 277). In Sweden, however, where the species is much less numerous, the majority of males are polyterritorial and most of the males obtain their two females in separate territories (TEMRIN 1984 and *in litt.*). Similar variation in type of territorial system in relation to density was found also in *Phylloscopus trochilus* (LAWN 1982, TIAINEN 1983) and in *Acrocephalus arundinaceus* (CATCHPOLE *et al.* 1985, DYRCZ 1986).

Final remarks

The main idea threading throughout the whole discussion can be expressed as follows: if we are to understand why polygyny occurs we cannot concentrate on studying only options available to one sex.

By studying thoroughly female choice we can learn a lot about mechanisms and criteria used by females to select mates but this will not suffice to explain the polygyny phenomenon. Similarly, by studying ways males apply to monopolize access to mates we can improve our understanding of *e.g.* territorial behaviour, but this will not give a full answer to the question: why polygyny occurs.

Only by recognizing that the occurrence of polygyny is a resultant of both inter- and intra- sexual selection; and by studying jointly both elements of this system can one hope to make a real progress.

A full explanation of the evolution of polygyny would also demand a thorough study of a whole set of ecological conditions and not only, as is usually done, limitations set upon birds by the situation in their breeding habitats. Factors which influence total population size (*cf T. troglodytes* — p. 296) or weather conditions along migration route (*cf P. sibilatrix* — p. 289) are to a large extent independent of the situation in the breeding habitats and the male/female interaction system, nevertheless they may be important in influencing the type of mating system one observes in the field.

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STRESZCZENIE

[Poligynia u trzech leśnych gatunków ptaków wróblowatych strefy umiarkowanej (wraz z krytycznym przeglądem hipotez dotyczących ewolucji poligynii)]

W latach 1976–79 badano systemy kojarzenia u świstunki leśnej *Phylloscopus sibilatrix*, pierwiosnka *Phylloscopus collybita* i strzyżyka *Troglodytes troglodytes*. Badania prowadzono w Białowieskim Parku Narodowym na dwóch powierzchniach próbnych — K i C. Powierzchnia K była porośnięta w większości łęgiem olszowo-jesionowym, niewielkie jej fragmenty pokrywał las grądowy. Powierzchnia C w całości znajdowała się w lesie grądowym.

Badane gatunki wykazywały liczne podobieństwa, ale różniły się wieloma aspektami biologii rozrodu, które mogły mieć wpływ na typ systemu kojarzenia (tab. 1). Różniły się też typem preferowanych siedlisk. Świstunki występowały w najwyższych zagęszczeniach w grądach, a pozostałe gatunki w łęgach (tab. 2).

U wszystkich gatunków stwierdzono występowanie poligynii (tab. 3 i 4). Była to zwykle bigamia, trigamię stwierdzono tylko trzykrotnie. Poligynia występowała w siedliskach, w których dany gatunek osiągnał wysokie zagęszczenia (por. tab. 2 z 3 i 4). Udział poligynicznych samców zmieniał się silnie między sezonami, wahając się od 0 do 40 %. W środowiskach o wysokim zagęszczeniu występowała zwykle niewielka nadwyżka samic.

Samce poligyniczne miały przeciętnie nieco większe terytoria niż samce monogamiczne (tab. 5), choć tylko w jednym przypadku różnica była statystycznie istotna. U świstunek nie stwierdzono różnic struktury siedliska w terytoriach samców mono- i poligynicznych (tab. 6). Podobnie u pierwiosnka gniazdującego w łęgu nie stwierdzono związku między szczegółami budowy siedliska a występowaniem poligynii. Ten sam fragment lasu mógł być zajmowany przez samotnego samca w jednym roku i przez bigamistę w roku następnym (ryc. 1).

Udatność kojarzenia samców wracających w kolejnych latach nie była stała. Ten sam samiec mógł być bigamistą w jednym roku i nie uzyskiwać żadnej samicy w roku następnym (tab. 7).

Partnerki samców poligynicznych osiedlały się zwykle w krótkim odstępie czasu. U świstunki i pierwiosnka w około 50 % przypadków odstęp czasu między osiedleniem się pierwszej i drugiej samicy wynosił 0–4 dni.

Udatność lęgów samców poligynicznych była dwu-, trzykrotnie wyższa niż

samców monogamicznych. Przeciętna udatność lęgów partnerek samców poligynicznych była równa (strzyżyk, pierwiosnek) lub nieco wyższa (świstunka) niż partnerek samców monogamicznych.

Poligynię u badanych gatunków wykazywano już wcześniej. Stosunkowo często u świstunki i strzyżyka, a sporadycznie u pierwiosnka, co jest sprzeczne z oczekiwaniami teoretycznymi, na podstawie których należałoby oczekiwać częstego występowania poligynii u pierwiosnka i jej braku lub sporadycznego tylko występowania u świstunki.

W dyskusji zrewidowano obecne poglądy teoretyczne dotyczące ewolucji poligynii. Dla wytłumaczenia tego zjawiska najczęściej proponowano model „progu poligynii" oparty na wyborze dokonywanym przez samice. Przetestowanie tego modelu jest obecnie niemożliwe ze względu na znaczne trudności metodyczne, ponieważ:

— założenie, że samice wybierają terytoria nie zostało jak dotąd potwierdzone;

— osiedlające się samice mogą dokonywać wyboru jedynie na podstawie oczekiwanego dostosowania, badacze mogą mierzyć jedynie zrealizowane dostosowanie; te dwie miary dostosowania nie muszą być ze sobą zgodne;

— istnieją różnice między próbkami samców, spośród których dokonuje wyboru samica, a próbką samców, których jakość ocenia obserwator (ryc. 2).

Modele wyboru partnerów dokonywanych przez samice są niewystarczające dla wyjaśnienia ewolucji poligynii, gdyż pomijają następujące fakty:

— proces osiedlania się samic jest najprawdopodobniej procesem hierarchicznym; samica musi najpierw zdecydować się, w jakim regionie geograficznym zakończyć wędrówkę, następnie wybrać siedlisko, a dopiero w ostatniej kolejności dokonać wyboru partnera. Wybory dokonywane na wcześniejszych etapach mogą bardzo silnie wpływać na to, czy poligynia wystąpi czy nie;

— samce nie są tylko pasywnymi obiektami, spośród których samice dokonują wyboru.

W systemie terytorialnym to konkurencja między samcami decyduje o tym, którym z nich uda się uzyskać terytorium. Ponieważ poligynia jest zwykle korzystna dla samców i — w najlepszym przypadku — neutralna dla samic, należy oczekiwać, że samce będą próbowały zmonopolizować dostęp do samic i tak zmienić sytuację, żeby zwiększyć swą szansę zostania wybranym przez samicę. Jest to możliwe do osiągnięcia przez obronę obszarów zawierających wiele zasobów, w siedliskach atrakcyjnych dla samic oraz wykluczenie części samców z posiadania terytoriów (ryc. 3). Wykluczenie części samców z rozrodu prowadzi do powstania ich lokalnego niedomiaru i wystąpienia poligynii (ryc. 4).

Obecne ramy teoretyczne są zbyt wąskie dla wyjaśnienia ewolucji poligynii. Pełne wyjaśnienie tego zjawiska wymagać będzie jednoczesnego rozpatrywania opcji reprodukcyjnych dostępnych dla każdej z płci, jak również ograniczeń ekologicznych wpływających na możliwość monopolizacji środowiska przez samce i wysokość kosztów ponoszonych przez samice.