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SIZE-DEPENDENT SELECTION ON ARRIVAL TIMES IN STICKLEBACKS: WHY SMALL MALES ARRIVE FIRST

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Abstract.—Studies on arrival time to breeding areas show that high-quality males usually arrive first and gain the highest reproductive success. This is generally assumed to be due to phenotype-dependent costs and benefits of early arrival. We show that the opposite arrival order can occur, probably due to selection on poor-quality males to increase their chances of reproduction. In a fish species, the threespine stickleback, *Gasterosteus aculeatus*, small males arrived before larger males at the breeding grounds. Early arrival was costly because predation risk was at its highest at the start of the season and early territory establishment was selected against, as demonstrated by selection coefficients for territory maintenance and hatching success. Large males probably postponed arrival until females were available to decrease predation risk costs and increase offspring production. An experimental study showed that a delay in arrival of large males does not decrease their probability of reproduction, because large males are able to take over nest sites from small males. Small males, on the other hand, are less likely to establish territories in competition with large males but can pay the costs of early arrival in exchange for the benefit of access to territories. Thus, whereas natural selection favors later arrival, sexual selection through competition for breeding territories favors early arrival in small, competitively inferior males. This results in the benefits of early arrival depending on the competitive ability of the male, which favors size-dependent optimal arrival times.

Key words.—Breeding phenology, condition dependence, fitness, male-male competition, migration, territory quality.

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In animals that reproduce in seasonal environments, high-quality males often arrive before low-quality males at breeding grounds and gain the highest reproductive success (e.g., Møller 1994; Aebischer et al. 1996; Lozano et al. 1996; Hasselquist 1998; Marra et al. 1998; Møller and de Lope 1999). This has been proposed to be due to the optimal arrival time varying among individuals depending on their phenotype, due to phenotype-dependent costs and benefits of early arrival (Price et al. 1988; Møller 1994, 2001; Kokko 1999). Possible costs of early arrival are reduced food intake and fecundity, reduced survival probability, and reduced offspring survival and growth if the offspring emerge too early (Møller 1994). Possible benefits of early arrival are access to the best territories or other resources, high mating success or mating with high-quality females (Møller 1994; Aebischer et al. 1996; Lozano et al. 1996; Hasselquist 1998; Gil and Slater 2000), and high offspring survival or growth rate (Verhulst and Tinbergen 1991; Landa 1992; Rowe et al. 1994; Wiggins et al. 1994; Hasselquist 1998; Einum and Fleming 2000). Generally, early arrival of high-quality males is assumed to be due to them being better able to pay the costs of early arrival than low-quality males (Verhulst et al. 1995; Svensson 1997).

Although most studies have found a positive condition-dependent arrival order, the opposite order with males in poor condition arriving first could occur if poor-condition males benefit more from early arrival than good-condition males, that is, if poor-condition males pay lower costs or gain higher benefits of early arrival as compared to later arrival, whereas good-condition males do not. The latter scenario, with poor-condition males gaining higher benefits, may occur if costs of early arrival select against too early arrival and the importance of priority depends on the competitive ability of the male (Broom et al. 1997, 2000; Kokko 1999). When males in good condition can take over the territory or mate of males in poor condition, then good-condition males may benefit by arriving later in the season if the cost of arrival is lower then. Males in poor condition, on the other hand, may do best by arriving early, before males of high competitive ability, and pay the high cost of early arrival in exchange for increased success in the competition for territories and mates. This presumes that poor-condition males either succeed in gaining some mating success before the competitively superior males arrive or that some of them are able to maintain their mate or territory when the rest of the males arrive, that is, that the priority effect sometimes overrides the competitive advantage. Thus, following a game theoretical reasoning, the optimal arrival time of an individual depends on what other individuals are doing as well as on their relative competitive ability (Iwasa et al. 1983; Parker and Courtney 1983; Thornhill and Alcock 1983; Zonneveld 1996; Holzapfel and Bradshaw 2002).

Most studies on timing of arrival have concentrated on phenotype-dependent costs of early arrival, whereas phenotype-dependent benefits have only rarely been considered. A few studies show that an inverse arrival order can occur and could arise due to phenotype-dependent benefits of early arrival. In some insect species, small males of poor competitive ability arrive (emerge) before large males of high competitive ability (Eberhard 1982; Thornhill and Alcock 1983; Alcock 1997). In the dusky warbler, *Phylloscopus fuscatus*, among males that occupied a territory in the previous autumn, small males arrive before large males, but the order is reversed among males that did not already occupy a territory (Forstmeier 2002).

Here, we investigated phenotype-dependent arrival and breeding times in the threespine stickleback, *Gasterosteus aculeatus*, in which body size influences success in the competition for territories and mates (Rowland 1989; Candolin 1998). In the investigated population, males have only one breeding season, at the age of two, during which they can breed repeatedly. The sticklebacks migrate to shallow coastal areas from deeper seawater as soon as the temperature of the water starts to rise in spring. Growth and survival conditions for offspring are more favorable in shallow water due to higher water temperature, high food availability, and perhaps fewer predators or more hiding places. In several breeding areas, sticklebacks arrive within a few weeks (Wootton 1976; Whoriskey and FitzGerald 1994), but the timing of arrival within this period has not been studied. A few investigations on other fish species show that fry hatching date influences fitness and that breeding time can be under directional (Einum and Fleming 2000) or stabilizing selection (Schultz 1993). However, other selective agents, such as arrival-dependent mortality risk of adults or arrival-dependent success in the competition for territories and matings have not been considered.

We investigated three different timing events: arrival to breeding areas, time of coming into breeding condition, and time of territory establishment (for males). These different events need not be strongly correlated, as different selection pressures could be operating during each event. To determine the different selection pressures that operate, we related size-dependent arrival and breeding times to the costs and benefits of arriving early. An important cost of early arrival is risk of predation, as terns arrive from their overwintering areas on the Southern Hemisphere at the same time as the first sticklebacks move to shallow water. Moreover, protective vegetation is scarce at the start of the season, which renders sticklebacks susceptible to predation. Predation risk is costly both through direct predation and indirectly through a negative effect of antipredator behavior on territory size (Candolin and Voigt 2001a), courtship activity, and mating success (Candolin 1997). Possible benefits of early arrival include the access to high-quality territories and females, especially because female encounter rate correlates with territory quality (Candolin and Voigt 2001a). However, late-arriving males of high competitive ability may be able to occupy the territory of males who arrived earlier, which could result in the benefit of early arrival to depend on the competitive ability of the male (Broom et al. 1997, 2000; Kokko 1999). Another possible benefit of early territory establishment is to bring forward the hatching time of offspring, which could increase offspring fitness or the number of breeding cycles that a male can complete in one season.

MATERIALS AND METHODS

Study Area

The study was carried out in Långskär and Vindskär Bays close to Tvärminne Zoological Station in the Baltic Sea in southern Finland (60°N, 23°E). The two bays are on different islands in the outer archipelago, separated by about 2 km. Långskär Bay is about 30 m long, 15 m wide and has a maximum depth of 1.5 m. Vindskär Bay is larger, about 100 m long, 50 m wide, and with a maximum depth of about 3 m. Both bays are in direct contact with the open sea. The habitat structure in both bays varies from open sand to dense algal growth (mainly *Fucus vesiculosus* and *Cladophora glomerata*). The predation pressure from terns (*Sterna hirundo* and *S. paradisaea*) is high in both bays. Fish predators are common in Vindskär Bay, especially perch (*Perca fluviatilis*) but have never been observed or caught in Långskär Bay, probably due to a narrow connection with the sea. Sticklebacks arrive in the bays at the beginning of May; adults disappear in July and juveniles stay until autumn. Males establish territories, build nests, and attract females for spawning. Females leave immediately after spawning and the male alone cares for the eggs and newly hatched fry for two to three weeks (Wootton 1976).

Temporal Variation in Size Distribution

We recorded the size-distribution of sticklebacks over the breeding season in Långskär Bay during two years, 1994 and 1996, and in Vindskär Bay during 1994. In 1994 fish were caught from 1 May to 18 July, and in 1996 from 1 May to 13 July, every second to fourth day, depending on weather conditions. We caught fish with transparent Plexiglas traps (20 × 20 × 40 cm) that had wings (20 × 60 cm) that directed fish toward the opening of the trap (1.5 × 20 cm; see Candolin and Voigt 2001b). In each bay we had four sampling areas, two with a low structural habitat complexity (about 25% of the area covered by stones and larger algae, mainly *F. vesiculosus*) and two with a high structural complexity (about 75% coverage). At each sampling area we caught sticklebacks from two different water depths, 30 cm and 80 cm, the 30-cm site being 1–3 m closer to the shore. We placed two traps at each water depth (16 traps in total per bay). The traps were set in the evening and collected the following day at noon. We measured the standard length of the fish and determined their sex when possible, that is, when the fish were in breeding condition and nuptially colored or gravid. The fish were released back at the site of capture after measurements, except during the first month of the season (May) in 1996, when we brought the fish to the laboratory for sex identification. No selectivity of the traps in relation to size of adult fish has been found when the catches of fish from traps have been compared to that by seining (U. Candolin, unpubl. data).

To analyze for predictors of the size of males in the bays during the first month of the breeding season (when fish were migrating into the bays), we fitted regression models with date, date^2, density of breeding males, and density of gravid females as independent variables. Terms that did not significantly improve the fit of the model were deleted in a backward stepwise mode. Year was added as a covariate for Långskär Bay to investigate for differences between years. The analysis is conservative when analyzing for changes in the size of arriving fish, because fish that arrived early were included in the samples caught later in the season. Furthermore, the analysis assumes that each individual can be regarded as an independent observation. The possibility exists that individuals of the same size are attracted to each other and caught in the same trap, which would increase the probability of a Type I error; thus, we also carried out the analyses on mean size of sticklebacks caught in each trap. Qualitatively similar results were obtained, which suggests that the assumption of independence was not significantly violated. Therefore, we present the results from the analyses with each individual as an independent observation.

Temporal Variation in Predation Risk Cost

We determined the predation risk from terns over the season in 1994 in Långskär Bay by noting the number of attacks during 1–2 h/day. Only attacks where the surface of the water was broken were recorded. Whether a tern managed to catch a stickleback could not always be reliable determined; therefore, we present only attack rate and not predation rate. We calculated predation risk per fish in the bay (i.e., attack rate per fish) by dividing attack rate with the number of fish caught in the traps on that day. The observations were made throughout the breeding season in the mornings of the days when the traps were emptied of fish.

Timing of Breeding and Reproductive Success

To determine the relationships between male size, time of territory establishment, maintenance of territory ownership, and reproductive success, we selected all males that established territories within a restricted area of Långskär Bay between 9–25 May 1996 and recorded their reproductive success. The chosen area is a preferred breeding area with a water depth of 40–70 cm and with a high density of sticklebacks. The time period includes both the first-arriving males and males that arrived later, when the density of fish was high and competition for territories intense. As soon as we observed a male that had established a territory, we marked the location of his territory on a map and determined its size by observing the male's behavior. Territory size was measured as length × width, as most territories stretched along large stones. We caught the male with a hand net and measured his standard length to the nearest millimeter. Before releasing the male back into his territory, we clipped the top of one of his dorsal spines so that he could be recognized in the future. All males resumed normal territorial behavior within half an hour from being released in the territory.

Fifteen to 18 days after the male had started to court females, when fry would be almost ready to hatch under the prevailing water temperatures (Wootton 1976), we collected the male's nest and transported it to the laboratory and counted the number of developed, healthy embryos. To make certain that we had collected the nest before any fry hatched, we checked the nest and the close surroundings for any hatched offspring. Fry stay close to the nest for a few days after hatching, while being guarded by the male. In all cases no hatched fry were found. We determined the expected hatching date by allowing the eggs to hatch in buckets with flowing water of the same temperature as in the field. The water flow served to keep the eggs aerated. We also caught the male to make sure that he was the same male that had established the territory. We did not know whether the male was the genetic father of all offspring, because sneak fertilizations occur in some stickleback populations (Goldschmidt and Bakker 1990; Rico et al. 1992), although not in all (Foster 1994). Therefore, the results could over- or underestimate the reproductive success of a male. However, the occurrence of sneak fertilizations is generally rare in sticklebacks (Goldschmidt and Bakker 1990; Rico et al. 1992; Foster 1994).

To determine whether selection for early territory establishment occurs through benefits in maintaining territory ownership or in number of hatched offspring, we calculated standardized linear selection differentials (s') and gradients (β') and standardized quadratic selection differentials (C') and gradients (γ') using simple and multivariate regression methods (Lande and Arnold 1983; Endler 1986). Univariate selection differentials describe the total selection on a trait (both direct and indirect), whereas selection gradients describe only the direct selection, by holding effects of other traits constant. We included male size and territory size in the analyses, as earlier studies have found both traits to influence mating success (reviewed by Rowland 1994; Whoriskey and FitzGerald 1994). The estimates of fitness—maintenance of territory ownership until the eggs were ready to hatch and number of eggs hatching—were converted to relative fitness with a mean of one (by dividing the individual fitness estimates by the mean of the sampled individuals). Each measured trait (date of territory establishment, body size, and territory size) was standardized to a mean of zero and a standard deviation of one. Linear selection differentials, s', and gradients, β', were calculated from linear models, $w = a + sz$ and $w = a + \Sigma \beta_i z_i$. Quadratic selection differentials, C', and gradients, γ', estimate the curvature of the selection functions, that is, whether stabilizing or disruptive selection occurs, and were calculated from models including quadratic terms. For gradients, we first calculated full models including quadratic terms and cross-product terms: $w = a + \Sigma \beta_i z_i + \Sigma \gamma_i z_i^2 + \Sigma \gamma_{ij} z_i z_j$, but deleted cross-product terms as the correlational selection gradients were small and nonsignificant. The residuals from the regression models were approximately normally distributed for hatching success (number of offspring hatching); we therefore obtained estimates for standard errors and significance of selection differentials and gradients from the regression models. For the maintenance of territory ownership the dependent variable is binary; we therefore obtained estimates for significance from logistic regression (Mitchell-Olds and Shaw 1987).

Effect of Body Size on Territory Ownership

To determine the effect of male size on the success in the competition for territories, we performed two experiments in 75-L aquaria in the laboratory. The males were caught from Långskär Bay in 1998 at the start of the season and maintained in holding aquaria under natural light conditions at 18°C before experimentation. The males could not build nests in the holding aquaria due to a lack of nesting material.

In the first experiment, we allowed two males of different size to compete for one nest site. We placed two males in reproductive condition (blue eyes) in an aquarium containing a nesting dish filled with sand, an artificial plant and some algae for nest construction. The smaller male was 4–24% (14% on average) smaller than the larger male measured as standard length. We left the males until one of them had built a nest. To determine whether the probability that the larger male would build a nest was determined by the size difference

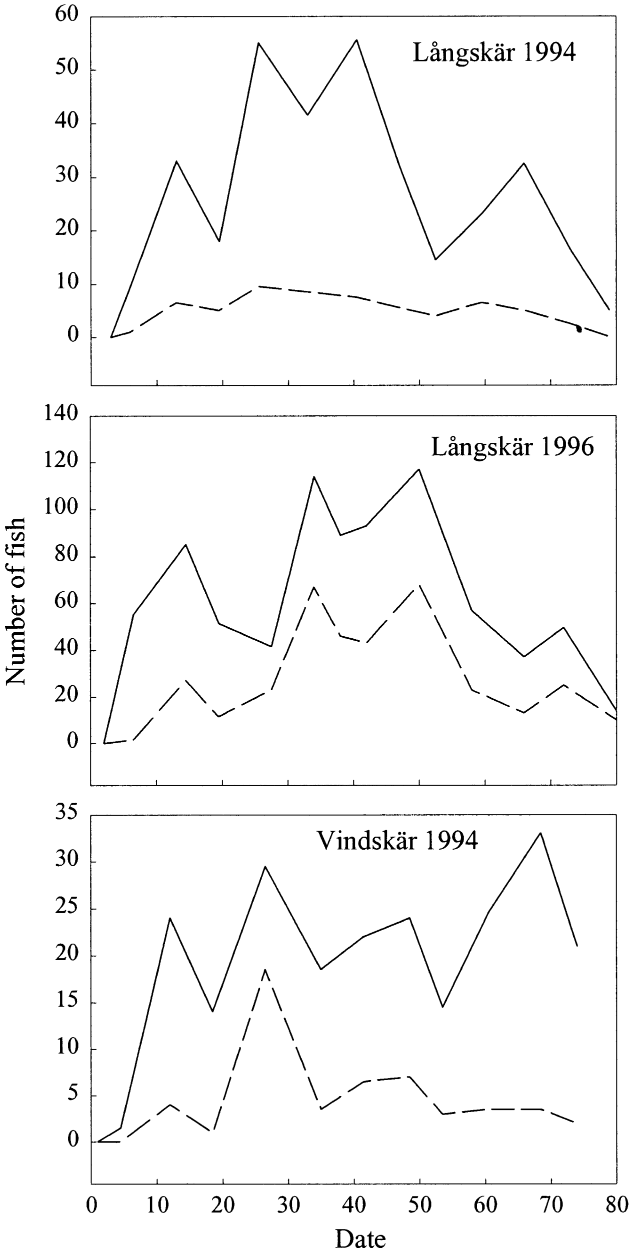

FIG. 1. Number of threespine sticklebacks caught in Långskär and Vindskär Bays, averaged over two sampling dates, during the breeding season. Solid lines: all fish; broken lines: males in breeding condition. Date 1 = 1 May.

between the males, we performed logistic regression. The size ratio (length of larger male/smaller male) was log transformed before analyses. We tested 16 different pairs of males.

In the second experiment, we determined the effect of size differences on the success in taking over a territory. We first allowed one male to build a nest in a nesting dish. Two days after nest completion, we introduced another male in reproductive condition and noted whether he succeeded in taking over the nest site from the first male. The intruding male differed in size from the resident male by −18% to +29%. We performed logistic regression to determine if absolute size or the size difference between the two males determined whether the intruder succeeded in taking over the nest. The size ratio (length of introduced male/territorial male) was log transformed before analyses. We tested 25 different male pairs.

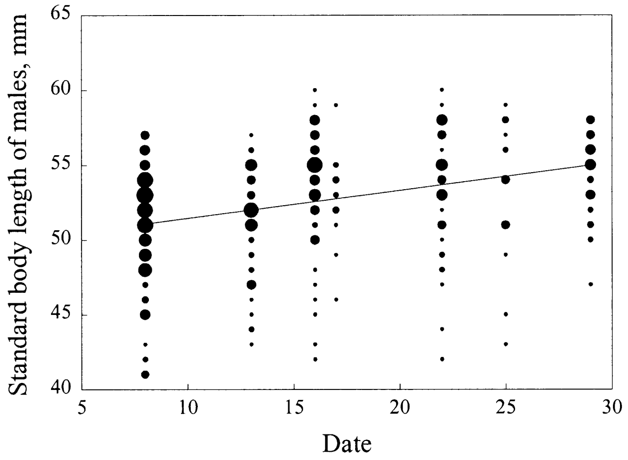

FIG. 2. Size of males in Långskär Bay in 1996 during the first month of the breeding season. $y = 49.61 + 0.19x$, Date 1 = 1 May.

RESULTS

Timing of Arrival and of Breeding

The first sticklebacks arrived in early May and the density of fish increased during the following month (Fig. 1). Males in breeding condition appeared a few days after the first fish had arrived and increased in density during the first month of the breeding season (Fig. 1). Small individuals arrived earlier than larger individuals: the mean size of sticklebacks caught in both bays increased during the first month, with the increase leveling of at the end of the month in Vindskär (Långskär: $r^2 = 0.09$, $b = 0.11$, $N = 729$, $t = 4.72$, $P < 0.001$, with year included as a significant factor; Vindskär: $r^2 = 0.13$, $b^2 = -0\ 06$, $N = 138$, $t = -4.08$, $P < 0.001$). The increase in size was too large to be due to growth (Wootton 1976).

A sex identification of the fish in 1996 revealed that small males arrived earlier than larger males, as the size of males increased with time (Fig. 2, Table 1A). The increase coincided with an increase in the density of breeding males (Table 1A). The size of females did not change with time ($F_{1,120} = 2.66$, $P > 0.1$), and the pattern differed from males ($F_{1,507} = 24.71$, $P < 0.001$). Females arrived later than males, as females were caught later during the first month of the season (males: day 15.3 ± 0.4 [SE], females: day 18.9 ± 0.6; $t_{509} = 5.05$, $P < 0.001$).

Small males came in breeding condition before larger males, as the size of males in breeding condition increased significantly during the first month of the breeding season (Fig. 3, Table 1B). In Långskär Bay, the increase in size was related to increased density of breeding males and to low density of gravid females (Table 1B); large males predominated later when the density of breeding males had increased but the density of gravid females was still low. In Vindskär Bay the sample size was much lower than in Långskär Bay, and no significant relationships to male or female densities

TABLE 1. Predictors of the size of threespine sticklebacks in Vindskär and Långskär Bays during the first month of the breeding season. The fish were sex identified in Långskär Bay in 1996.

	Långskär 1994 and 1996		Vindskär 1994	
	t	P	t	P
A. All males in 1996				
Date	3.65*	<0.001*		
Date^2	−0.64	0.519		
Density of breeding males	3.05*	0.002*		
Density of gravid females	1.03	0.304		
Final model	$r^2 = 0.14$, $F_{2,386} = 30.53$, $P < 0.001$			
B. Males in breeding condition				
Date	4.06*	<0.001*	3.26*	0.003*
Date^2	−3.60*	0.001*	−0.46	0.650
Density of breeding males	3.50*	0.001*	−0.88	0.387
Density of gravid females	−2.01*	0.046*	0.29	0.775
Year	4.08*	<0.001*		
Final model	$r^2 = 0.22$, $F_{5,163} = 9.44$, $P < 0.001$		$r^2 = 0.31$, $F_{1,24} = 10.60$, $P = 0.003$	

* Variables that were included in the final model.

were found (Table 1B). Gravid females appeared about 10 days later than males in breeding condition in both bays and both years.

Size of Fish over the Whole Season

Over the whole breeding season, from early May to mid-July, large sticklebacks dominated in the middle of the season in both Långskär Bay ($r^2 = 0.06$, $b^2 = -0.001$, $N = 1792$, $t = -4.37$, $P < 0.001$, year was included as a significant factor in the model) and Vindskär Bay ($r^2 = 0.03$, $b^2 = -0.006$, $N = 427$, $t = -3.69$, $P < 0.001$). Among breeding males, large males dominated in the middle of the season in Långskär Bay ($r^2 = 0.04$, $b^2 = -0.002$, $N = 548$, $t = -3.57$, $P < 0.001$). In Vindskär Bay, large males tended to dominate in the middle of the season ($r^2 = 0.13$, $b^2 = -0.001$, $N = 80$, $t = -1.69$, $P = 0.09$), but the density of breeding males was the main predictor of male size ($b = 0.27$, $t = 1.99$, $P = 0.050$): size increased with male density. In Långskär Bay, size increased with the density of breeding males when only density of breeding males and year were included in the models ($r^2 = 0.02$, $b = 0.02$, $t = 2.30$, $P = 0.022$). Thus, in both bays small males predominated when the density of competing males was low.

Temporal Variation in Predation Risk Cost

Predation pressure decreased with time in Långskär Bay in 1994, both when it comes to absolute attack rate ($r^2 = 0.45$, $b = -0.04$, $F_{1,22} = 17.1$, $P < 0.001$) and attack rate per fish ($r^2 = 0.38$, $b = -0.01$, $F_{1,22} = 12.77$, $P = 0.002$). Over the whole season, from beginning of May to mid-July, the size of sticklebacks depended negatively on predator attack rate per fish, although the variation explained by predation pressure was low ($r^2 = 0.01$, $b = -8.34$, $F_{1,665} = 6.48$, $P = 0.011$): small individuals predominated when predation pressure was at its highest at the start of the season, whereas larger individuals predominated later when predation pressure was lower.

Timing of Breeding and Reproductive Success

The first territorial males were observed at the same time as the first males in breeding condition were caught, a few days after the first fish had arrived in the bays. Males that established territories early in the season were smaller than

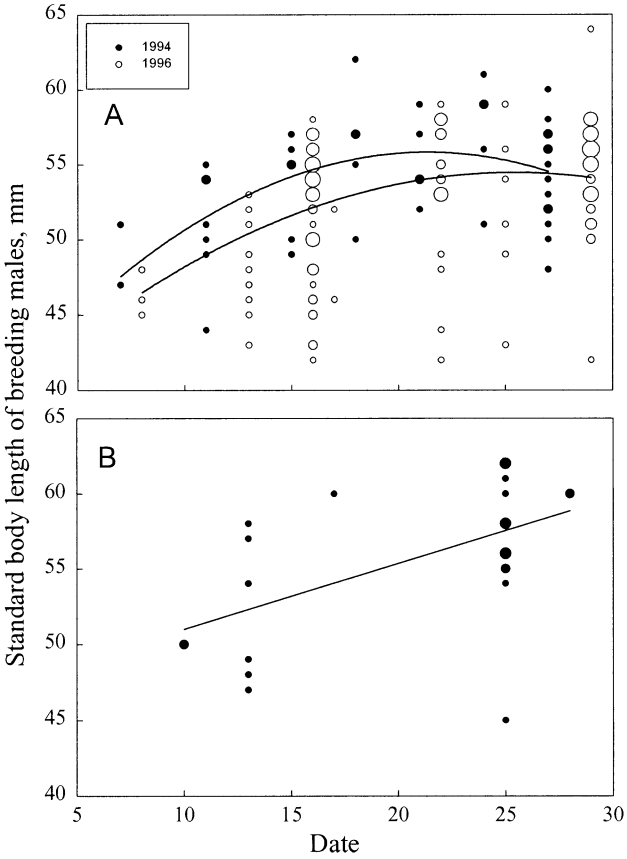

FIG. 3. Size of males in breeding condition (A) in Långskär Bay, 1994: $y = 37.55 + 1.71x - 0.04x^2$; 1996: $y = 37.45 + 1.34x - 0.03x^2$; and (B) in Vindskär Bay during the first month of the breeding season, $y = 46.63 + 0.44x$. Date 1 = 1 May.

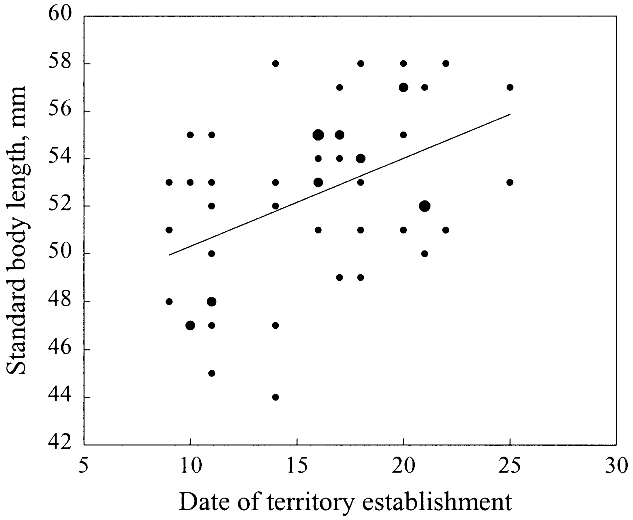

FIG. 4. Size of males establishing territories between 9–25 May in Långskär Bay in 1996, $y = 46.61 + 0.37x$.

males that established territories later ($r^2 = 0.21$, $F_{1,50} = 13.20$, $P = 0.001$, Fig. 4). The probability of maintaining territory ownership until the eggs were almost ready to hatch, when they were collected by us, increased with later territory establishment, larger male size and, weakly, with larger territory size (Table 2). However, only large body size showed a tendency to be directly related to the probability of maintaining territory ownership (Table 3).

Selection for increased hatching success favored later territory establishment, larger male size, and larger territories (Table 2). However, in contrast to territory ownership, male size was only indirectly related to hatching success, whereas date of territory establishment and size of territory directly influenced hatching success (Table 3). A tendency toward stabilizing selection for male size was detected (Table 3). Thus, we found no indication of early territory establishment increasing the probability of maintaining a territory or increasing hatching success.

Males that established territories early tended to have an earlier hatching date ($r^2 = 0.08$, $b = 0.16$, $F_{1,37} = 3.41$, $P = 0.073$). However, the difference in hatching date between the first and the last laid egg clutches was only 9 days, while the difference in territory establishment date was 16 days. This is due to males that established territories early having to wait until gravid females appeared before they could receive eggs. The temperature showed no sharp increases but was constantly between 10–12°C during the study period, until the beginning of June, when it slowly started to increase.

Effect of Body Size on Territory Ownership

Male size determined success in the competition for nest sites in the first experiment: the probability that the larger male would win increased with size disparity between males (logistic regression, $\chi^2 = 8.1$, df = 1, $P = 0.004$, Fig. 5A). In the second experiment, the probability that an intruder would succeed in taking over a territory increased the larger the intruder was in relation to the territorial male ($\chi^2 = 23.3$, df = 1, $P < 0.001$, Fig. 5B), and with increased absolute size of the intruder ($\chi^2 = 4.6$, df = 1, $P = 0.034$). Thus, small males are at a disadvantage in the competition for nest sites, and large males can succeed in taking over a nest site from a smaller male if no sites are available when they arrive.

DISCUSSION

Small males arrived at the breeding areas, came in breeding condition, and established territories before larger males. The change in the size of males cannot be due to growth due to the short time period (Wootton 1976). Moreover, males stop growing during the breeding season and instead lose weight, as food intake rate is reduced during breeding and energy is allocated to reproductive activities, such as territory establishment and courtship (Chellappa et al. 1989, 1995; Candolin 2000).

It is likely that large males postponed breeding until predation pressure from terns had decreased and gravid females had started to appear. This is supported by large males in breeding condition predominating when predation pressure from terns had decreased and algae (mainly *C. glomerata*) that provides hiding places from terns had grown up. The density of competing males was then high, but the aquarium experiments suggest that large males are able to take over territories from smaller males if no territories are available when they arrive. The density of gravid females was still low, as males entered breeding condition before the density of gravid females increased, as expected by protandry models (Wiklund and Fagerström 1977; Bulmer 1983; Iwasa et al.

TABLE 2. Standardized linear (s') and quadratic (C') selection differentials for breeding characteristics (date of territory establishment, body size, and territory size) of male sticklebacks establishing territories between 9–25 May. Maintenance of territory ownership and hatching success as fitness measures ($N = 52$).

	Linear selection		Quadratic selection	
	s' (SE)	P	C' (SE)	P
Territory ownership				
Date	0.16 (0.07)	0.034	−0.03 (0.07)	0.871
Male size	0.22 (0.07)	0.006	−0.05 (0.06)	0.887
Territory size	0.14 (0.07)	0.064	−0.03 (0.06)	0.971
Hatching success				
Date	0.43 (0.10)	<0.001	−0.04 (0.10)	0.701
Male size	0.39 (0.10)	<0.001	−0.03 (0.09)	0.758
Territory size	0.40 (0.10)	<0.001	0.01 (0.09)	0.878

TABLE 3. Standardized linear (β′) and quadratic (γ′) selection gradients for breeding characteristics (date of territory establishment, body size, and territory size) of male sticklebacks establishing territories between 9–25 May. Maintenance of territory ownership and hatching success as fitness measures ($N = 52$).

	Linear selection		Quadratic selection	
	β′ (SE)	*P*	γ′ (SE)	*P*
Territory ownership				
Date	.08 (0.07)	0.248	−0.02 (0.07)	0.915
Male size	0.18 (0.09)	0.077	−0.05 (0.06)	0.900
Territory size	0.02 (0.08)	0.534	−0.01 (0.06)	0.987
Hatching success				
Date	0.32 (0.10)	0.001	−0.09 (0.09)	0.334
Male size	0.12 (0.11)	0.286	−0.13 (0.08)	0.099
Territory size	0.25 (0.10)	0.019	0.06 (0.08)	0.446

1983; Parker and Courtney 1983; Thornhill and Alcock 1983; Zonneveld 1996; Morbey 2002).

Whether small males also arrived and entered breeding condition later than larger males is not known, but it appears unlikely. The proportion of small males in the catches increased after the peak in breeding activity, at the end of May and beginning of June, but the density of fish did not increase. Thus, migration into the bays seems to have been restricted to the first month of the season.

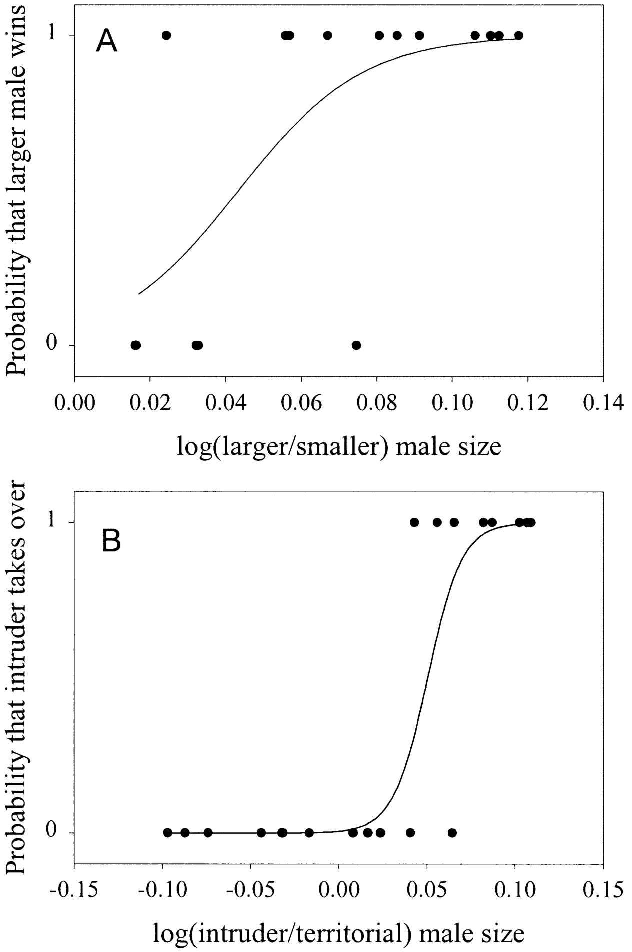

FIG. 5. The dependence of the probability that (A) a larger male would occupy a nest site, and (B) that an intruder male would take over a nest site, on the size disparity between the males.

Benefits of Early Arrival for Territory Maintenance and Hatching Success

The cost of early arrival in terms of increased predation risk implies that there must be some benefit of early arrival for small males that outweighs the cost. Selection analysis found no benefit of early territory establishment for the maintenance of territory ownership or number of hatched offspring. In contrast, males that established territories at the height of the season had a higher hatching success than males that established territories early in the season. This could be due to males that established territories later in the season experiencing less competition during territory maintenance than males that established territories early and had to defend their territory against the large number of males that arrived after them. Alternatively, it could be due to quality differences other than male size confounding an effect of time on hatching success, due to the correlative nature of the data. It is possible that males that established territories at the height of the breeding season were attractive males preferred by females (high mating success) or good fathers that managed to hatch a large proportion of the eggs that they tended. Males that established territories at the start of the season might have had an even worse hatching success had they established territories at the height of the season. On the other hand, there was no significant correlational selection on body size and breeding time, but this could similarly be due to the correlative nature of the data, with males that established territories later doing better due to quality differences other than body size. Thus, the possibility cannot be completely excluded that some males benefited from early territory establishment by increasing their mating success.

Another possible benefit of early arrival and breeding is to bring forward the time of hatching. However, whereas the difference in the time of territory establishment was up to 16 days, the difference in hatching time was at best 9 days. This may not be a large advantage when it comes to increasing the number of breeding cycles that a male can complete in one season. A breeding cycle lasts for about 20 days at the experimental temperature (Wootton 1976), and the breeding season lasts for almost 3 months in the study area. There were no sharp increases in the water temperature that would have increased the benefit of hatching at a particular time. Moreover, hatching too early could be disadvantageous if it reduces growth rate, due to cold water, and prolongs the time that offspring are susceptible to predation and cannibalism. Thus, a slightly earlier hatching date is unlikely to be the major factor favoring early arrival of small males.

Benefits of Early Arrival in the Competition for Territories

The aquarium experiments suggest that small males benefited from early arrival in improving their success in the competition for territories. The density of sticklebacks is high in the bays, and competition for territories is intense during the peak of the breeding season (Candolin and Voigt 2001a). A small male has a low probability of establishing a territory in competition with a larger male, as demonstrated by the aquarium experiment (see also Larson 1976; Rowland 1983, 1989). In contrast, a large male can expel a small male from a nest site if no other sites are available. Thus, small males may do best by arriving early and establishing territories while the density of large males is low. This is further supported by the negative relationship between male size and the density of breeding males in the field. Small males timed their arrival and breeding to times of low male density and, thus, to low intensity of competition. However, for success in the competition for territories to favor early arrival of small males, some small males must be able to maintain their territories when larger males arrive. This possibility may increase if small males manage to gain egg clutches and enter the parental phase before the density of large males increases. Males become less active when entering the parental phase, which makes them less conspicuous to other males. Moreover, the size of the territories decreases during the parental phase (U. Candolin, pers. obs.), which frees up some space for later-arriving males and increases the number of males that can breed in a given area. However, the selection analyses found no benefit of earlier territory establishment for maintaining territory ownership. Again this might be due to the correlative nature of the data with males that are more likely to maintain their territories under competition establishing territories later in the season.

Small males dominated after the peak in breeding activity. Large males were most active for a few weeks when they established their territories and courted females, after which they reduced their activity level and entered the parental phase. Small males, on the other hand, were active at all times of the season. This can be due to small males being less successful in establishing and maintaining a territory and in gaining matings and entering the parental phase, and therefore spending more time attempting to establish territories and attracting females. This lends further support to the finding that small males are at a disadvantage in the competition for territories and matings and therefore have to arrive early.

Taken together the results suggest that small males are doing the ''best of a bad job'' in establishing territories early in the season when predation pressure is high and the density of females low. The possibility remains, however, that small males are less susceptible to terns than larger males and therefore experience lower costs of early arrival. This is contradicted by the finding that small fish are generally more vulnerable to predation, due to gape-limitation of predators, and may be easier to handle and escape less often after capture (Fuiman and Magurran 1994; Sogard 1997). Moreover, a study on refuge use suggests that small sticklebacks are subject to higher predation risk from birds than larger sticklebacks (Krause et al. 1998). Thus, it appears unlikely that small males would experience a significantly lower predation risk and that this would have favored their earlier arrival and breeding times.

Evolutionary Consequences

Size-dependent selection on arrival time may not result in an evolutionary response, as male size may be largely environmentally determined through hatching date. Males can complete several cycles in one season and offspring of one male hatch at different times of the season and reach different adult sizes. Nevertheless, size-dependent selection on arrival time may spread out the optimal breeding times and give a larger proportion of the population a chance to breed. Traits other than male size may then become more important in determining male mating success. These traits might be more closely associated with male genetic quality than body size.

Comparison to Other Species

The time-dependent size distribution of sticklebacks differs from what has been found in many other species, especially birds, where high-quality males usually arrive and breed first (see introduction). There are several possible, nonexclusive explanations to why sticklebacks in our population differ from the general pattern among other species. First, the priority effect may occur but be weaker than in other investigated species where late-arriving individuals do not challenge earlier arriving individuals (e.g., Krebs 1982; Jakobsson 1988; Tobias 1997). In sticklebacks, a large male can take over the territory of a smaller male, but some small males probably succeed in maintaining their territory when the larger males arrive. Thus, the priority effect sometimes overrides a large size advantage, which could explain the occurrence of size-dependent breeding times. Second, the availability of territories may be more limited than in many other species where territories are still available for late-arriving individuals, although they may be of low quality. Third, territories of sticklebacks decrease in size when males enter the parental phase. This increases the number of territories that can exist, which gives low-quality males a chance to breed if they establish large courtship territories under low male density and small parental-care territories under high male density. Fourth, migration costs are probably low for sticklebacks, as they only migrate from deep to shallow water. In several bird species, high cost of migration prevents males in poor condition from arriving early, resulting in a positive condition-dependent arrival order (Møller 1994; Kokko 1999). Other costs of early arrival, such as reduced food intake and fecundity, that promote a positive condition-dependent arrival order in other species, could similarly be low or not differ between small and large stickleback males.

In conclusion, this study shows that small males generally arrive and enter breeding condition before larger males. This is probably the best strategy of small competitively inferior males as they pay high costs of early arrival, in terms of high predation risk and low hatching success, in exchange for the benefit of access to territories. Thus, whereas natural selection favors later arrival, sexual selection through competition for breeding territories favors early arrival in small, competitively inferior males and promotes the evolution of size-dependent optimal arrival times.

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LITERATURE CITED

Aebischer, A., N. Perrin, M. Krieg, J. Studer, and D. R. Meyer. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler *Locustella luscinioides*. J. Avian Biol. 27:143–152.

Alcock, J. 1997. Small males emerge earlier than large males in Dawson's burrowing bee (*Amegilla dawsoni*) (Hymenoptera: Anthophorini). J. Zool. 242:453–462.

Broom, M., C. Cannings, and G. T. Vickers. 1997. A sequential-arrivals model of territory acquisition. J. Theor. Biol 189: 257–272.

———. 2000. A sequential-arrivals model of territory acquisition II. J. Theor. Biol. 207:389–403.

Bulmer, M. G. 1983. Models for the evolution of protandry in insects. Theor. Popul. Biol. 23:314–322.

Candolin, U. 1997. Predation risk affects courtship and attractiveness of competing threespine stickleback males. Behav. Ecol. Sociobiol. 41:81–87.

———. 1998. Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. Proc. R. Soc. Lond. B 265:1171–1175.

———. 2000. Changes in expression and honesty of sexual signalling over the reproductive lifetime of sticklebacks. Proc. R. Soc. Lond. B 267:2425–2430.

Candolin, U., and H.-R. Voigt. 2001a. Correlation between male size and territory quality: consequence of male competition or predation risk? Oikos 95:225–230.

———. 2001b. No effect of a parasite on reproduction in stickleback males: a laboratory artefact? Parasitology 122:457–464.

Chellappa, S., F. A. Huntingford, R. H. C. Strang, and R. Y. Thomson. 1989. Annual variation in energy reserves in male three-spined stickleback, *Gasterosteus aculeatus* L. (Pisces, Gasterosteidae). J. Fish Biol. 35:275–286.

———. 1995. Condition factor and hepatosomatic index as estimates of energy status in male three-spined stickleback. J. Fish Biol. 47:775–787.

Eberhard, W. G. 1982. Beetle horn dimorphism: making the best of a bad lot. Am. Nat. 119:420–426.

Einum, S., and I. A. Fleming. 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). Evolution 54:628–639.

Endler, J. A. 1986. Natural selection in the wild. Princeton Univ. Press, Princeton, NJ.

Forstmeier, W. 2002. Benefits of early arrival at breeding grounds vary between males. J. Anim. Ecol. 71:1–9.

Foster, S. A. 1994. Evolution of the reproductive behaviour of threespine stickleback. Pp 381–398 *in* M. A. Bell and S. A. Foster, eds. The evolutionary biology of the threespine stickleback. Oxford Univ. Press, Oxford, U.K.

Fuiman, L. A., and A. E. Magurran. 1994. Development of predator defences in fishes. Rev. Fish Biol. Fish. 4:145–183.

Gil, D., and P. J. B. Slater. 2000. Multiple song repertoire characteristics in the willow warbler (*Phylloscopus trochilus*): correlations with female choice and offspring viability. Behav. Ecol. Sociobiol. 47:319–326.

Goldschmidt, T., and T. C. M. Bakker. 1990. Determinants of reproductive success of male sticklebacks in the field and in the laboratory. Neth. J. Zool. 40:664–687.

Hasselquist, D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. Ecology 79: 2376–2390.

Holzapfel, C. M., and W. E. Bradshaw. 2002. Protandry: The relationship between emergence time and male fitness in the pitcher-plant mosquito. Ecology 83:607–611.

Iwasa, Y., J. F. Odendaal, D. D. Murphy, P. R. Ehrlich, and A. E. Launer. 1983. ESS emergence pattern of male butterflies in stochastic environments. Evol. Ecol. 8:503–523.

Jakobsson, S. 1988. Territorial fidelity of willow warbler (*Phylloscopus trochilus*) males and success in competition over territories. Behav. Ecol. Sociobiol. 22:79–84.

Kokko, H. 1999. Competition for early arrival in migratory birds. J. Anim. Ecol. 68:940–950.

Krause, J., S. P. Loader, J. McDermott, and G. D. Ruxton. 1998. Refuge use by fish as a function of body length-related metabolic expenditure and predation risk. Proc. R. Soc. Lond. B 265: 2373–2379.

Krebs, J. R. 1982. Territorial defense in the great tit (*Parus major*): Do residents always win? Behav. Ecol. Sociobiol. 11:185–194.

Landa, K. 1992. Seasonal declines in offspring fitness and selection for early reproduction in nymph-overwintering grasshoppers. Evolution 46:121–135.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Larson, G. L. 1976. Social behavior and feeding ability of two phenotypes of *Gasterosteus aculeatus* in relation to their spatial and trophic segregation in a temperate lake. Can. J. Zool. 54: 107–121.

Lozano, G. A., S. Perreault, and R. E. Lemon. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. J. Avian Biol. 27:164–170.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Mitchell-Olds, T., and R. G. Shaw. 1987. Regression analysis of natural selection: statistical interference and biological interpretation. Evolution 41:1149–1161.

Møller, A. P. 1994. Phenotype dependent arrival time and its consequences in a migratory bird. Behav. Ecol. Sociobiol. 35: 115–122.

———. 2001. Heritability of arrival date in a migratory bird. Proc. R. Soc. Lond. B 268:203–206.

Møller, A. P., and F. de Lope. 1999. Senescence in a short-lived migratory bird: age-dependent morphology, migration, reproduction and parasitism. J. Anim. Ecol. 68:163–171.

Morbey, Y. E. 2002. Protandry models and their application to salmon. Behav. Ecol. 13:337–343.

Parker, G. A., and S. P. Courtney. 1983. Seasonal incidence: adaptive variation in the timing of life history stages. J. Theor. Biol. 105:147–155.

Price, T., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. Science 240: 798–799.

Rico, C., U. Kuhnlein, and G. J. FitzGerald. 1992. Male reproductive tactics in the threespine stickleback: an evaluation by DNA fingerprinting. Mol. Ecol. 1:79–87.

Rowe, L., D. Ludwig, and D. Schluter. 1994. Time, condition, and the seasonal decline of avian clutch size. Am. Nat. 143:698–722.

Rowland, W. J. 1983. Interspecific aggression and dominance in *Gasterosteus*. Env. Biol. Fishes 8:269–277.

———. 1989. The effects of body size, aggression and nuptial coloration on competition for territories in male threespine sticklebacks, *Gasterosteus aculeatus*. Anim. Behav. 132:282–289.

———. 1994. Proximate determinants of stickleback behaviour: an evolutionary perspective. Pp. 297–344 *in* M. A. Bell and S. A. Foster, eds. The evolutionary biology of the threespine stickleback. Oxford Univ. Press, Oxford, U.K.

Schultz, E. T. 1993. The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformes, Embiotocidae). Evolution 47:520–539.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60:1129–1157.

Svensson, E. 1997. Natural selection on avian breeding time: causality, fecundity- dependent, and fecundity-independent selection. Evolution 51:1276–1283.

Thornhill, R., and J. Alcock. 1983. The evolution of insect mating systems. Harvard Univ. Press, Cambridge, MA.

Tobias, J. 1997. Asymmetric territorial contests in the European robin: the role of settlement costs. Anim. Behav. 54:9–21.

Verhulst, S., and J. M. Tinbergen. 1991. Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus major*. J. Anim. Ecol. 60:269–282.

Verhulst, S., J. H. Van Balen, and J. M. Tinbergen. 1995. Seasonal decline in reproductive success of the great tit: variation in time or quality. Ecology 76:2392–2403.

Whoriskey, F. G., and G. J. FitzGerald. 1994. Ecology of the threespine stickleback on the breeding grounds. Pp. 189–206 *in* M. A. Bell and S. A. Foster, eds. The evolutionary biology of the threespine stickleback. Oxford Univ. Press, Oxford, U.K.

Wiggins, D. A., T. Part, and L. Gustafsson. 1994. Seasonal decline in collared flycatcher *Ficedula albicollis* reproductive success: an experimental approach. Oikos 70:359–364.

Wiklund, C., and T. Fagerström. 1977. Why do males emerge before females? Oecologia 31:153–158.

Wootton, R. J. 1976. The biology of the sticklebacks. Academic Press, London.

Zonneveld, C. 1996. Being big or emerging early? Polyandry and the trade-off between size and emergence in male butterflies. Am. Nat. 147:946–965.

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