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REVIEW

Protandrous arrival timing to breeding areas: a review

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Abstract

Protandry, the earlier arrival of males to breeding areas than females, is a common pattern of sex-biased timing in many animal taxa (e.g. some insects, fish, amphibians, reptiles, birds and mammals). The adaptive significance of protandry is not fully understood and, since the 1970s, at least seven hypotheses for protandry have been proposed. We describe each of these hypotheses and summarize what is known about each. In three of these hypotheses, the relative arrival timing of males and females has no direct fitness consequences for males or females, but selection for different timing in each sex indirectly produces protandry. In the other four hypotheses, the difference between male and female timing has fitness consequences for males or females and selection directly maintains the fitness-maximizing degree of sex-biased timing. The hypotheses are not mutually exclusive, and the degree of multiple mating by males and the occurrence of male territoriality seem to determine the relative importance of each hypothesis. In order to understand the adaptive significance of sex-biased timing, future studies need to consider all the alternatives and to assess the costs and benefits to males of early arrival relative to calendar date, to other males and to females.

Keywords

Arrival timing, behavioural ecology, breeding schedule, emergence, migration, protandry, protogyny.

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INTRODUCTION

In a diverse array of animal taxa, males and females arrive at breeding areas according to different schedules. Protandry, the more common form of sex-biased arrival timing, occurs when males arrive at breeding areas earlier in the season on average than females (e.g. arthropods: Thornhill & Alcock 1983; ground squirrels: Michener 1984; birds: Francis & Cooke 1986; nematodes: Grewal *et al.* 1993). The term "arrive" is used here in a general sense. For example, male butterflies may emerge from pupae as reproductive adults earlier on average than females (e.g. Wiklund & Fagerström 1977). In birds breeding at temperate latitudes, males may migrate and arrive at breeding areas earlier on average than females (e.g. Myers 1981). Protogyny, the earlier arrival of females than males, is a less common form of sex-biased arrival timing exhibited by some birds with sex role reversal (e.g. Oring & Lank 1982; Reynolds *et al.* 1986). "Pioneering" is another term used in the literature, and refers to the first sex to exploit or colonize breeding habitat (e.g. Harari *et al.* 2000). We favour the terms protandry and protogyny over pioneering because of their greater generality.

The term protandry is also used in the literature to refer to similar timing phenomena. In plants, protandry in sexual function occurs commonly within or among flowers (Richards 1986). This is similar to the earlier onset of male sexual function in hermaphroditic animals (e.g. Charnov 1982) and, in both cases, the timing of sexual function can be viewed as an allocation problem within a single individual. We restrict our discussion to sex-biased arrival timing in animal populations, although the ideas developed here may be relevant to understanding these other forms of protandry.

We first describe and name the hypotheses for protandry, which can be divided into two classes (Table 1). In the first class, the timing of males relative to females has no direct fitness consequences for males or females. Instead, selection acts independently on the arrival timing of each sex, either directly or indirectly on a correlated character, and so indirectly produces sex-biased arrival (e.g.

Table 1 Seven hypotheses for protandry (the earlier arrival of males to breeding areas than females). Selection either acts indirectly or directly on the difference between male and female arrival timing. These hypotheses can also be adapted to explain protogyny (the earlier arrival of females to breeding areas than males).

Hypothesis	Form of selection	Selective causation	Key references
Rank advantage	Indirect	Selection among the territorial sex (males) to be earlier than other males	Ketterson & Nolan (1976); Myers (1981)
Susceptibility	Indirect	Stronger selection on females than on males to avoid adverse environmental conditions early in the year	Ketterson & Nolan (1983); Francis & Cooke (1986)
Constraint	Indirect	Stronger selection on a trait correlated with earlier arrival in males than in females	Gauthreaux (1978); Wiklund & Solbreck (1982)
Mate opportunity	Direct	Selection on males to arrive earlier than females to maximize their mating opportunities	Wiklund & Fagerström (1977); Bulmer (1983a); Iwasa *et al.* (1983); Parker & Courtney (1983)
Waiting cost	Direct	Selection on females to arrive later than males to minimize their time spent waiting for males	Fagerström & Wiklund (1982); Michener (1984); Olsson & Madsen (1996)
Mate choice	Direct	Selection on females to arrive later than males as a mate assessment strategy	Wang *et al.* (1990); Wedell (1992)
Outbreeding	Direct	Selection on males to arrive earlier than females to avoid mating among closely related individuals	Petersen (1892) in Wedell (1992)

Wiklund & Solbreck 1982). For example, greater selection for larger size in female than in male insects may result in the prolonged development and later emergence of females (Wiklund & Solbreck 1982). In the second class, the difference between male and female arrival timing has fitness consequences for males or females and selection directly maintains sex-biased timing. For example, protandry may allow polygynous male butterflies to maximize mating opportunities with monogamous females (e.g. Wiklund & Fagerström 1977; Iwasa *et al.* 1983). The hypotheses in both classes can also be adapted to explain protogyny.

We then assess each hypothesis for several taxonomic groups, including arthropods, birds, reptiles, amphibians, salmon and ground squirrels. We show that the study of protandry has proceeded somewhat independently in different taxa, possibly because different hypotheses are more suited to some mating systems than to others. A final objective is to generalize how mating systems influence the ecological function of protandry. We suggest that the adaptive function of sex-biased timing is not yet fully understood, and that future studies would benefit by considering all the alternatives.

INDIRECT SELECTION HYPOTHESES

Indirect selection hypotheses assume direct selection on arrival timing or on traits related to arrival timing within sexes, but not on the relative arrival timing between sexes. Protandry is an incidental consequence of selection acting directly, but independently, on the arrival timing of each sex. The three hypotheses described here differ in the trait that selection is presumed to act upon, and in the constraints on arrival timing.

Rank advantage hypothesis

In birds, protandry may occur because competition for territories selects for the earliest arriving males (Ketterson & Nolan 1976; Myers 1981). The arrival timing of males can be interpreted as an evolutionary game (*sensu* Maynard Smith 1982), because the quality of territory obtained depends on the number of prior arrivals. This type of competition advances the arrival of all males to a point (cf. Kokko 1999). Presumably, male arrival timing (and hence the degree of protandry) is set by the benefits of attaining a high-quality territory and by the costs of arriving early in the season. The costs and benefits of arriving earlier than females are not considered. Under this hypothesis, protogyny should occur under sex role reversal.

Susceptibility hypothesis

Adverse environmental conditions on the breeding grounds may select for protandry if the sexes are differentially susceptible. For example, males may be larger than females and thus better able to cope with poor conditions that prevail early in the year (Ketterson & Nolan 1983; Francis & Cooke 1986; cf. Møller 1994). This hypothesis assumes similar benefits to each sex for early arrival relative to calendar date, but different costs. The degree of protandry should depend on how severely the environmental conditions affect males and females. Selection would favour protogyny if males were more susceptible to adverse environmental conditions early in the breeding season than females.

Constraint hypothesis

Selection may act indirectly on arrival timing through selection on some trait other than arrival timing. For example, migratory timing constraints may cause protandry in birds (Gauthreaux 1978). If males are selected to winter farther north than females, but migrate at the same time and same rate (the constraint), males will arrive at breeding areas sooner than females. Wiklund & Solbreck (1982) propose an analogous hypothesis for protandry in butterflies: if males are selected to be small relative to females, but develop at similar rates to females (the constraint), protandry results. This hypothesis also could be adapted to explain protogyny. For example, protogyny would result if female birds are selected to winter farther north than males, but migrate at the same rate as males.

Under the constraint hypothesis, sex-biased arrival timing may be maladaptive. Rejecting an adaptive hypothesis for protandry in favour of a constraint hypothesis is difficult because cause and effect may be confounded in the latter. For example, if males migrate at the same time and rate as females, then selection for protandrous arrival may favour males who winter farther north than females (Ketterson & Nolan 1976). Likewise, selection for protandry in butterflies may favour a shorter development period and smaller size among males than among females. Demonstrating the absence of a putative constraint, for example by showing plasticity in migratory rate, is the most effective way to discredit this hypothesis.

The three hypotheses discussed so far are not mutually exclusive. Any combination of benefits, costs and constraints that act differentially on males and females could lead to protandry (or protogyny). A hypothesis would be considered indirect if arrival relative to the other sex was not the target of selection.

DIRECT SELECTION HYPOTHESES

Direct selection hypotheses for protandry assume that the relative arrival timing of males and females has fitness consequences for males or females. We consider four hypotheses of this type. Selection is assumed to act upon males in the first hypothesis and on females in the second and third hypotheses. The fourth considers the benefits of outbreeding to both sexes.

Mate opportunity hypothesis

Protandry may allow polygynous males to maximize their opportunities to mate with females (Scott 1977; Wiklund & Fagerström 1977). The "butterfly emergence game" is the prototype model of this hypothesis (Bulmer 1983a; Iwasa *et al.* 1983; Parker & Courtney 1983), and such models predict when males should emerge relative to an expected female emergence distribution. During each day of the emergence period, males engage in scramble competition for unmated females emerging on that day and divide the number of matings equally. The models assume that the female emergence distribution is fixed, that females mate immediately after emergence and that all females mate. Bulmer (1983b) also modelled the timing of production of male and female reproductives in annual social Hymenoptera under the same hypothesis. Under the mate opportunity hypothesis, selection would favour protogyny if females mated more frequently than males within a breeding season.

Predictions of arrival timing under this hypothesis have been made using both game theoretic (e.g. Bulmer 1983a; Iwasa *et al.* 1983; Zonneveld & Metz 1991) and simpler optimization (e.g. Wiklund & Fagerström 1977) approaches. The former seeks the stable arrival distribution, whereas the latter seeks an optimal mean arrival date with a fixed standard deviation. In both cases, the fitness-maximizing degree of protandry is a tradeoff between female availability, the reduction in mating opportunities caused by the presence of competitors or death. Under Iwasa *et al.*'s (1983) game theoretic approach, all males have equal fitness regardless of arrival date, but this is not the case under the optimization approach, nor under Zonneveld & Metz's (1991) game theoretic approach.

Under the mate opportunity hypothesis, the degree of protandry depends on factors that influence mating opportunities. For example, if males experience high mortality rates after arrival to breeding areas, they will be exposed to females for only a short period. Consequently, their arrival should closely track female availability. If postarrival mortality rates are low and males can expect to live for the entire breeding season, all males should arrive on the first day of the season and be highly protandrous (Scott 1977; Botterweg 1982; Bulmer 1983a; Iwasa *et al.* 1983; Parker & Courtney 1983; Thornhill & Alcock 1983).

The availability of females and their fecundity also affects protandry. Less protandry is favoured when females are polyandrous, because the peak of female availability is shifted to later in the season (Parker & Courtney 1983; Zonneveld 1992). Greater protandry is expected when early arriving females have higher fecundity (Kleckner *et al.* 1995) or when mating with virgins is advantageous (Wiklund & Fagerström 1977; Thornhill & Alcock 1983; Wedell 1992; Zonneveld

1992, 1996a; Simmons *et al.* 1994). Mating with virgins could be advantageous if female fecundity decreases with successive bouts of egg-laying or if sperm competition favours the first male to mate with a polyandrous female. We do not consider the virgin mating advantage hypothesis and the mate opportunity hypothesis as competing alternatives, although others do (Wedell 1992; Simmons *et al.* 1994).

Male territoriality could also promote protandry (Thornhill & Alcock 1983; Wang *et al.* 1990) if, by being first, males acquire territories that contain more female emergence sites or encounter sites (Elgar & Pierce 1988; Wang *et al.* 1990). This scenario differs from the rank advantage hypothesis because the timing of males relative to females has fitness consequences. If encounter rates with females are low or if prereproductive death of females is possible, there should be less protandry (Zonneveld & Metz 1991; but see Botterweg 1982). Finally, protandry should be greater in populations with discrete rather than with overlapping generations (Singer 1982). With overlapping generations, arriving early would confer less of a mating advantage because late arriving males would also be early arrivals in the following breeding period.

Previous models of protandry in insects consider how the benefits of large male size, attained through prolonged development, reduce optimal protandry (Zonneveld 1996a, b). Size can also influence a male's access to females. Alcock (1997) suggests that small male burrowing bees, *Amegilla dawsoni*, who are at a competitive disadvantage, may emerge earlier than larger males to avoid competition with larger males. Consequently, the proportions of large and small males in the population should influence when males arrive relative to females. Male size may also influence protandry if size influences longevity or success in territorial disputes (Thornhill & Alcock 1983).

Clearly, the details of the mating system are important for developing quantitative predictions of protandry under the mate opportunity hypothesis. It is also important to consider the constraints that may act on arrival timing. For example, optimal protandry may not be realized in a given year because of unpredictable female timing (e.g. Tatar 1984; Iwasa & Haccou 1994). Also, there could be a tradeoff between emerging or arriving early and acquiring large size among males (Zonneveld 1996a, b).

Waiting cost hypothesis

This hypothesis considers the selective advantage of protandry from the female's perspective. The phase preceding arrival is assumed to be safer or energetically cheaper than the breeding season. Upon arrival at breeding areas, males may be unable to reproduce immediately if they must first search for females or spend a minimum amount of time in physiological or behavioural preparations (Fagerström & Wiklund 1982; Lederhouse *et al.* 1982; Michener 1984; Olsson & Madsen 1996; Wiklund *et al.* 1996; Taylor *et al.* 1998). Such preparations could include reproductive maturation or the establishment of territories or dominance hierarchies. If females must wait until males are ready to reproduce, delaying arrival and spending more time in the prearrival phase would be less costly than waiting for males at breeding areas. For example, in parasites or other organisms that use hosts for breeding, males are responsible for finding the host and attracting females (e.g. Grewal *et al.* 1993). By arriving (i.e. emerging into the reproductive phase) later than males, females may avoid waiting for males to become established. Under this hypothesis, greater protandry should be observed when waiting costs are higher. Protogyny would be expected if males must wait for females before breeding.

If females must wait to be encountered by searching males, females may be selected to minimize their waiting time by matching the period with the highest number of searching males. Protandry is favoured in a polygynous mating system with female monogamy because peak male searching occurs later than peak male emergence, whereas peak female availability occurs during peak female emergence (Scott 1977; Fagerström & Wiklund 1982; Zonneveld & Metz 1991). According to the models of Zonneveld & Metz (1991), protandry can be consistent with both the maximization of mating opportunities by males and the minimization of waiting time by females. There is only a small difference in the optimal degree of protandry from the male and female perspectives. Even if males were monogamous, protandry would probably facilitate less waiting time by females. This shows that the direct selection hypotheses are not mutually exclusive.

Mate choice hypothesis

Protandry may also result from a strategy whereby females select and mate with males that have survived the longest (i.e. the highest quality males) (Wang *et al.* 1990; Wedell 1992). Under this hypothesis, females must be able to assess male longevity (time since arrival) and higher quality males must have a higher survival probability than lower quality males (i.e. mortality cannot occur randomly). Postarrival waiting by females must also be more costly than delaying arrival. The degree of protandry depends on the benefits of mate choice and on the costs of waiting. Protogyny would be expected under sex role reversal.

A similar idea could explain protandry in taxa with high survival rates during the breeding season. If long-term defence of a breeding territory or rank within a dominance hierarchy (or lek) sorts out the highest quality males, and if females can assess the duration of successful defence (e. g. black grouse, *Tetrao tetrix*: Kokko *et al.* 1999), protandry could reduce waiting costs while facilitating mate choice. Dunn & Cockburn's (1999) study of superb fairy-wrens, *Malurus cyaneus*, provides an example in which females can assess male quality based on a timing criterion (time since moult).

Outbreeding hypothesis

Protandry may also be a strategy to facilitate outbreeding in insects (Petersen 1892 in Wedell 1992). This idea is similar to protandry as a selfing avoidance strategy in plants (Richards 1986). By dispersing from a common rearing environment into reproductive phase before nearby, related females, males may increase the likelihood of mating with unrelated females. This hypothesis has been discredited because it does not explain why protandry would be favoured over protogyny (see Wiklund & Fagerström 1977). This hypothesis applies less well to longer lived species (such as birds, fish, amphibians, reptiles or mammals) because the earlier departure of males from the prebreeding stage will not necessarily affect the relatedness of potential mates.

TESTING THE HYPOTHESES

In reviewing the literature on protandry, a taxonomic bias in the hypotheses considered becomes apparent. Studies investigating the emergence timing of male and female arthropods mostly pit the mate opportunity hypothesis against the constraint hypothesis. In contrast, the less numerous avian studies usually focus on the rank advantage hypothesis. Less attention has been paid to protandry in amphibians, reptiles, fish and mammals, although these studies have contributed some novel ideas about possible adaptive functions of protandry. Many of the alternative hypotheses for protandry tend to be ignored in individual studies, possibly because differences in mating systems or differences in the selective regimes that act on males and females may affect the relative importance of each hypothesis. Several selective factors may also operate simultaneously to varying degrees (cf. Kokko 1999).

In order to help clarify what is known about each hypothesis and to identify gaps in our knowledge, we assess the evidence for each hypothesis, categorized by taxa and by the approach taken. Some studies evaluate one or several hypotheses by assessing the underlying assumptions of each. Others test specific predictions by comparing protandry among populations or among different generations of the same population (e.g. Wiklund & Forsberg 1991). Finally, a few test a single hypothesis (specifically the mate opportunity hypothesis) by comparing observed protandry to protandry predicted by models (e.g. Sawada *et al.* 1997). The use of the proper units for protandry (days vs. degree-days) is an important issue for such comparative studies, and is discussed by Tatar (1984).

Protandry in arthropods

Protandry is a common feature of solitary insects with non-overlapping generations, and also occurs in annual social Hymenoptera and spiders (e.g. Evans & West-Eberhard 1970; Botterweg 1982; Thornhill & Alcock 1983; Vollrath 1987; Gunnarsson & Johnsson 1990; Wang *et al.* 1990; McDonald & Borden 1995; Bourke 1997; Bradshaw *et al.* 1997; Mayer & Miliczky 1998; Kranz *et al.* 1999). Protandry also occurs at short time scales (Parker 1970a; Pompanon *et al.* 1995; Alcock 1997; Harari *et al.* 2000). For example, male dung flies, *Scatophaga stercoraria*, arrive at fresh cow droppings, where mating takes place, before females (Parker 1970a).

A unique kind of protandry occurs in the eusocial thrips, *Kladothrips hamiltoni*. In this gall-inducing species, a single female foundress first produces a non-dispersing generation (soldiers) and then the foundress and sib-mated soldiers produce a second, dispersing generation (Kranz *et al.* 1999). Male soldiers tend to be produced before female soldiers, and the unfertilized eggs of female soldiers produce male dispersers and fertilized eggs produce female dispersers. The foundress is more closely related to her granddaughters than to her grandsons, and female soldiers are more closely related to their daughters than to their sons. The earlier production of male soldiers may maximize the probability that newly eclosing female soldiers will mate quickly and produce female progeny to comprise the dispersing generation (Kranz *et al.* 1999). This hypothesis bears the closest similarity to the waiting cost hypothesis because of the presumed costs to females of delayed mating. However, unlike the other hypotheses discussed, this hypothesis does not consider the optimal timing of individual males and females. Although protandry in the production of males and females differs substantially from protandry in arrival timing, the ideas we have reviewed may be of use in future studies examining the adaptive significance of protandry in thrips.

Of the indirect selection hypotheses, only the constraint hypothesis has received significant attention in the arthropod literature. The rank advantage hypothesis ignores any direct benefits of multiple mating by males and so, by itself, may not apply broadly to arthropods. However, in a study of territorial grasshoppers, *Ligurotettix coquilletti*, Wang *et al.* (1990) observed selection for the earliest arriving males because they acquired higher quality territories which attracted more females. The susceptibility hypothesis has been ignored, but when male arthropods are smaller than females, which is often the case, they should not arrive earlier than females under this hypothesis.

The constraint hypothesis often has been discredited as the sole cause of protandry in butterflies because evidence for fixed development rates is weak (Wiklund & Solbreck

1982; Wiklund *et al.* 1991, 1992; Nylin *et al.* 1993; Nylin 1994). For example, in partially bivoltine butterflies (*Pieris napi*, *P. rapae*, *Polygonia c-album* and *Pararge aegeria*), Wiklund *et al.* (1992) observed a greater propensity for males to enter diapause than females as the season progressed. Protandry in the second, directly developing generation was due, in part, to this developmental flexibility. In a different butterfly (*Leptidea sinapis*) study, Wiklund & Solbreck (1982) showed that protandry was facilitated through a greater difference among male and female pupal development times in the overwintering generation than in the non-diapausing generation. Other studies discredit the constraint hypothesis because protandry cannot be explained by size differences alone (e.g. grasshoppers, *L. coquilletti*: Wang *et al.* 1990) or because males are larger than females (e.g. spiders, *Pityohyphantes phrygianus*: Gunnarsson & Johnsson 1990; bushcrickets, *Requena verticalis*: Simmons *et al.* 1994).

Of the direct selection hypotheses, the mate opportunity hypothesis has received most attention in the arthropod literature. This is probably because it emphasizes the benefits of multiple mating by males. In many arthropods, males invest little besides sperm in each mating event, and consequently mating with several females can greatly increase male reproductive success (Thornhill & Alcock 1983). Several studies claim support for the mate opportunity hypothesis because the assumptions appear to be met (e.g. *S. stercoraria*: Parker 1970b; *L. coquilletti*: Wang *et al.* 1990; bumble bees, *Bombus* spp.: Bourke 1997). Other studies support the mate opportunity hypothesis (or more generally a direct selection hypothesis) when one or more competing alternatives are discredited (e.g. *P. phrygianus*: Gunnarsson & Johnsson 1990; *P. napi*: Wiklund *et al.* 1991; butterflies, *Brassolis sophorae*: Carvalho *et al.* 1998).

Several predictions of the mate opportunity hypothesis have been tested. Under Iwasa *et al.*'s (1983) model, the mate opportunity hypothesis predicts equal fitness regardless of arrival date, at least when no constraints are imposed on the arrival distribution of males. This prediction has received qualitative (e.g. *L. sinapis*: Wiklund & Solbreck 1982) and statistical (e.g. butterflies, *Euphydryas editha*: Baughman 1991) support. However, other studies have detected selection for the earlier arrival of males and therefore protandry (in some years in wasps, *Sphecius grandis*: Hastings 1989; *B. sophorae*: Carvalho *et al.* 1998; grasshoppers, *Sphenarium purpurascens*: Cueva del Castillo & Núñez-Fárfán 1999; but see Masumoto 1994), which counters the equal fitness prediction. Testing for equal fitness, however, can be problematic because the results depend strongly on statistical power.

All the direct selection hypotheses, including the mate opportunity hypothesis, predict protandry in insects regardless of whether or not they diapause prior to reaching adulthood. This prediction is generally upheld. Butterflies without pupal diapause have similar protandry to those that overwinter as pupae (Wiklund & Solbreck 1982; Nylin *et al.* 1993) or as adults in reproductive diapause (Wiklund *et al.* 1996). Singer's (1982) prediction that protandry should be greater in species with discrete generations than with overlapping generations is also consistent with all the direct selection hypotheses. Some studies support this prediction by observing greater protandry in species with discrete rather than overlapping generations (e.g. butterflies: Nylin *et al.* 1993), but other studies do not (e.g. mosquitoes, *Wyeomia smithii*: Bradshaw *et al.* 1997).

Specific predictions about the effect of ecological factors on protandry have been tested less frequently. Consistent with theory, the high degree of protandry in the butterfly, *Gonepteryx rhamni*, may be due to its relatively prolonged longevity (Wiklund *et al.* 1996). Greater protandry was observed under higher densities in mosquitoes (*Aedes sierrensis*: Kleckner *et al.* 1995; *W. smithii*: Bradshaw *et al.* 1997), which is consistent with Zonneveld & Metz's (1991) model. However, this result also suggests the presence of developmental constraints. Higher larval densities and thus lower food availability may result in a greater size difference among the sexes and consequently greater protandry (Kleckner *et al.* 1995; Bradshaw *et al.* 1997). As another example of a tradeoff between early arrival and prolonged development, males of a partially bivoltine butterfly, *P. napi*, appear to favour prolonged development over protandrous emergence in the time-constrained, directly developing generation (Wiklund *et al.* 1991).

Polyandry should reduce protandry under the mate opportunity hypothesis, and this prediction is supported in butterflies (Wiklund & Forsberg 1991). However, selection for large male size, relative to other males, in polyandrous mating systems may also reduce protandry (Wiklund & Forsberg 1991; Zonneveld 1996a). In fact, Zonneveld (1992) could not account for the observed amount of protandry through polyandry alone, suggesting that selection for larger males was important. Also, Wiklund & Forsberg's (1991) observation of less protandry with greater polyandry was apparent only in the diapausing generation when developmental constraints were absent. In contrast to these studies, Cueva del Castillo & Núñez-Fárfán (1999) detected significant correlational selection acting simultaneously on protandry and large body size in male polyandrous grasshoppers, *S. purpurascens*, so that the earliest emerging males were also the largest. Their results imply that protandrous males experienced accelerated development.

Finally, some studies have compared observed protandry to protandry predicted by models of the mate opportunity hypothesis. Observed protandry closely matched theoretical predictions in some studies (*E. editha*: Iwasa *et al.* 1983; *A. sierrensis*: Kleckner *et al.* 1995; butterflies, *Anthocharis scolymus*: Sawada *et al.* 1997), but not in others (butterflies, *Papilio polyxenes*: Lederhouse *et al.* 1982; *E. editha*: Baughman *et al.* 1988; onion maggots, *Delia antiqua*: McDonald & Borden 1995). However, only Sawada *et al.* (1997) used statistics to support their conclusion, and such comparisons can be difficult to interpret due to statistical problems or inaccurate model predictions. The degree of similarity between observed and predicted protandry provides little information about a single hypothesis, because low statistical power increases the risk of not rejecting a false null hypothesis. The results also depend strongly on the accuracy of the model. If the parameters used by the model are inaccurate, misleading predictions can lead to the rejection of a true null hypothesis.

Less attention has been given to alternative direct selection hypotheses for protandry. Wang *et al.* (1990) considered the waiting cost hypothesis and the mate choice hypothesis in their study of grasshoppers, *L. coquilletti*. In arthropods, the waiting cost hypothesis considers the risk of prereproductive mortality to females while waiting to be encountered by searching males. In Wang *et al.*'s study, prereproductive death of females in the absence of protandry seemed highly unlikely and so was inconsistent with the waiting cost hypothesis. The mate choice hypothesis was not supported because females probably could not assess male longevity. The outbreeding hypothesis has not been evaluated in arthropods.

Protandry in birds

In birds, protandry has been widely reported during migration to breeding areas in a large number of passerines and non-passerines (e.g. Myers 1981, and references therein; references in Gauthreaux 1982; Ketterson & Nolan 1983; Francis & Cooke 1986, and references therein; Moore *et al.* 1990; Calder & Calder 1994; Otahal 1995, and references therein). Protogynous arrival occurs less frequently than protandry, and has been reported for several sex role-reversed species, including spotted sandpipers, *Actitis macularia*, red-necked phalaropes, *Phalaropus lobatus*, and Wilson's phalaropes, *P. tricolor* (Oring & Lank 1982; Reynolds *et al.* 1986). Simultaneous arrival at breeding areas also occurs in some species (e.g. snow geese, *Chen caerulescens*: Cooke *et al.* 1975; brewer's blackbirds, *Euphagus cyanocephalus*: Orians 1980; red phalaropes, *P. fulicarius*, and sanderlings, *Calidris alba*: Myers 1981).

Several indirect selection hypotheses have been considered in studies of sex-biased arrival timing in birds. The susceptibility hypothesis probably plays a minor role. This hypothesis could not explain protandry in warblers during spring migration because similar sized males and females migrated at similar times (Francis & Cooke 1986). Also, the larger sex does not necessarily arrive earlier in shorebirds (see table 4 in Myers 1981). However, Nisbet & Medway (1972) propose that the susceptibility hypothesis may operate in concert with the rank advantage hypothesis in great reed warblers, *Acrocephalus orientalis*.

The constraint hypothesis also lacks strong support in avian studies. Francis & Cooke's (1986) warbler study is inconsistent with the constraint hypothesis because the earlier sex does not necessarily winter farther north. Myers (1981) found a correlation between protandry and wintering latitude using data for eight bird species, but discounted the constraint hypothesis. Instead, Myers suggested that the wintering distribution was a proximate mechanism to facilitate the earlier arrival of males to breeding areas than females.

The rank advantage hypothesis has received wide support in the avian literature because the territorial sex generally arrives earlier than the non-territorial sex (Myers 1981; Oring & Lank 1982; Francis & Cooke 1986). Furthermore, simultaneous arrival of males and females has been observed in species without a territorial sex or very little competition for territories (sanderling: Parmalee 1970; red phalarope: Connors *et al.* 1979; Myers 1981). The rank advantage hypothesis cannot be the sole explanation for sex-biased timing in birds, however, because Reynolds *et al.* (1986) observed protogyny in two species of phalaropes without territorial females.

Of the direct selection hypotheses for protandry, only the mate opportunity hypothesis has received some attention in the avian literature. Reynolds *et al.* (1986) suggested that female phalaropes arrived earlier than males to maximize their probability of obtaining a mate, or several mates under polyandry. Francis & Cooke (1990) also suggested that the earlier arrival of male than female rose-breasted grosbeaks, *Pheucticus ludovicianus*, would increase a male's probability of obtaining a mate early in the season. The acquisition of high-quality territories can also contribute to increased mating opportunities for males. For example, earlier settling male great reed warblers mated with more females because they acquired higher quality territories (Hasselquist 1998).

Protandry in other taxa

Protandry has been documented in salmon (*Oncorhynchus* spp.: Morbey 2000), amphibians (*Notophthalmus viridescens*: Hurlbert 1969; *Ambystoma jeffersonianum*: Douglas 1979; *A. talpoideum*: Semlitsch 1985; Semlitsch *et al.* 1993), snakes (*Thamnophis sirtalis*, *Vipera berus*: Gregory 1974, and references therein), lizards (*Lacerta vivipara*, *L. agilis*: van Damme *et al.* 1987; *L. agilis*: Olsson & Madsen 1996) and ground squirrels (Sciuridae: Michener 1983, 1984). For each of these groups, we present a few key conclusions that relate to the ultimate causation of protandry.

Morbey (2000) favoured the mate opportunity hypothesis in salmon primarily because males are polygynous and are reproductively active for a longer period than females. Mate choice may also play a minor role, because it may take time for males to establish dominance hierarchies. However, it is unclear whether females would suffer costs if they waited on the spawning grounds instead of delaying arrival. The remaining alternative hypotheses for protandry are inconsistent with the biology of salmon and with observed patterns of protandry (Morbey 2000).

In amphibians, protandrous arrival to breeding ponds is also thought to allow males to maximize mating opportunities, especially when female timing is unpredictable (Douglas 1979; Semlitsch *et al.* 1993). Likewise, in ground squirrels, protandrous emergence of ground squirrels from hibernation probably allows males to maximize mating opportunities, especially with virgin females (Michener 1983). The absence of protandry among non-breeding males is consistent with this hypothesis (Michener 1983). Female ground squirrels may also benefit from protandry because male–male competition may sort out the highest quality males or there may be a greater selection of males to choose from when mating late (Michener 1984).

The several snake studies support the waiting cost hypothesis, although waiting may occur for different reasons. In garter snakes, *T. sirtalis*, males search for females during a short mating season, and protandry during posthibernation emergence may maximize the probability that females are encountered and mated by males (Gregory 1974). In *V. berus*, postemergent males require more time than females to mature and protandrous emergence may minimize waiting time by females (Volsøe 1944 in Gregory 1974). In an experimental study of lizards, *L. agilis*, that reproduce soon after emergence from hibernation, females became receptive to mating sooner when paired with an early emerged male than with a late emerged male (Olsson & Madsen 1996). Upon emergence from hibernation, males are not yet ready to mate and early emerging females may risk mating with these infertile males. Alternative hypotheses for protandry in snakes have received little attention.

CONCLUSIONS

Protandry is a common feature of life histories with restricted breeding seasons. This fact suggests that protandry is a reproductive strategy, but the selective advantages of protandry have been difficult to demonstrate conclusively. Often, alternative hypotheses make the same prediction about how an ecological factor (e.g. polyandry) should affect protandry. Assessing how well observed protandry matches theoretical protandry depends on the accuracy of the predictions and on statistical power. Quantitative predictions have been developed for the mate opportunity hypothesis only, and often the models have not considered all the factors influencing mating opportunities (e.g. mortality schedule, longevity, degree of polygyny and polyandry, territoriality, sperm competition and temporal variation in female fecundity). Studies that test hypotheses for protandry may also fail if timing cannot be fine-tuned to local ecological or social conditions. The observed amount of protandry may reflect a bet hedging strategy to expected ecological and social conditions that have been selected for over evolutionary time (Iwasa & Haccou 1994). Finally, any hypothesis is almost certainly incapable of explaining protandry in all taxa and under all circumstances.

Despite these difficulties, several conclusions can be drawn about the adaptive significance of protandry. In species with semelparity (some arthropods and salmon) and a greater frequency of mating in males than females (arthropods, salmon, amphibians, snakes and ground squirrels), the current evidence suggests that selection acts directly on protandry. In arthropods, salmon, amphibians and ground squirrels, the most important contributing factor selecting for protandry seems to be the maximization of mating opportunities with females, especially virgin females. In snakes, protandry probably allows females to minimize waiting costs. However, other benefits of protandry (namely the maximization of mating opportunities by males) have not been assessed in snakes.

In birds, differential selection on the arrival timing of each sex appears to be more important then direct selection on the relative timing of males and females. The rank advantage hypothesis appears to be the most important factor selecting for sex-biased timing. This difference between taxa probably relates to the different intensity of selection on multiple mating in each taxa. If there is strong selection to mate several times (as there would be in males that do not invest more than sperm), timing relative to females is critical. In birds with a greater tendency towards monogamy, there should be greater selection on characters that will improve mate quality rather than mate quantity. In particular, acquiring a high-quality territory by arriving early may be of critical importance for attracting high-quality females or for supporting the demands of raising offspring. However, growing evidence suggests that selection may also act directly on the difference in male and female arrival timing in birds. If high-quality territories help in acquiring more mates, both the rank advantage hypothesis and the mate opportunity hypothesis may operate together, but to different degrees. This would also be true in other taxa with territorial males.

The degree of polygamy within a breeding season seems to be the most important clue to the primary cause of sex-biased timing. However, because the function of protandry also depends on the taxonomic grouping, future studies are needed to determine whether this conclusion holds within a taxon. It is noteworthy that protandrous arrival to breeding areas is a common feature of hummingbirds, many of which are promiscuous (e.g. Calder & Calder 1994). Perhaps experiments would support the mate opportunity hypothesis in this group of birds.

Future studies attempting to identify the adaptive function of protandry need to consider the many possible benefits of protandry (cf. Kokko 1999). In particular, arthropod studies need to consider the rank advantage hypothesis and avian studies need to consider direct selection hypotheses. One way to assess the relative importance of each alternative hypothesis is to clarify the predictions each hypothesis makes by modelling. Currently, only the mate opportunity hypothesis has received significant theoretical treatment. Differential timing may be better understood if the costs and benefits of early arrival, relative to calendar date and relative to both sexes, are assessed for the species under investigation.

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BIOSKETCH

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