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## *Life-history strategies and the effectiveness of sexual selection*

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**Summary.** The hypothesized relationship between the relative strength of sexual selection and life-history strategies is reexamined. The potential effectiveness of sexual selection depends not only on the relative survivorship of immature stages, but also on other components of fitness. The effects of fecundity and timing of maturation must be evaluated together with the survivorship in order to determine the responsiveness of alternative life-history configurations to the force of sexual selection. Moreover, the r-K continuum is an inadequate model for comparisons of life-history strategies. A general three-dimensional demographic model provides a more comprehensive conceptual framework for life-history comparisons. The three-parameter demographic model is similar to several earlier two-dimensional life-history schemes and appears to describe a broad spectrum of the life-history strategies exhibited in nature. Most higher taxa tend to be dominated by only one or two of the three endpoint strategies: "equilibrium" (large investment in relatively few individual offspring), "opportunistic" (small size and rapid maturation), and "periodic" (pulsed production of large numbers of small offspring). A survey of teleost fishes and examples from several other higher taxa supports McLain's (1991) contention that the strength of sexual selection is influenced by life-history strategy. Conspicuous males are common among relative equilibrium and opportunistic strategists, but are essentially absent among species associated with the high-fecundity, periodic reproductive strategy. The absence of sexually selected traits in high-fecundity broadcast spawners implies that differential survivorship among immature life stages is nonrandom in all cases.

### **Selection on life stages**

In a recent FORUM contribution, McLain (1991) postulated that the relative strength of sexual selection may depend upon the life-history strategy. Here sexual selection is equated with differential mating success and its effect on the evolution of traits with no apparent survival value or even negative survival value. The idea seems to have merit, because directional selection on a phenotype is primarily associated with the life cycle

stage with the smallest average fitness (Arnold and Wade 1984). I reexamine McLain's hypothesis and offer two refinements to the problem.

McLain focused attention entirely on the effects of differential juvenile survivorship, and noted that the life stage with lowest survivorship makes the largest contribution to total variation in lifetime reproductive success (LRS). According to Brown (1988), the overall variance in lifetime reproductive success among breeders and nonbreeders can be partitioned into two components, the proportion due to variance among individuals that breed and the proportion due to complete failure to breed. These two components comprise the right half of the equation.

$$\text{Total variation in LRS} = pV(\text{LRS}) + p(1-p)\overline{\text{LRS}}^2 \quad (1)$$

in which  $V(\text{LRS})$  is the variance in lifetime reproductive success,  $p$  is the proportion of adults that actually breed, and  $\overline{\text{LRS}}^2$  is the squared mean lifetime reproductive success. In this case, LRS is estimated from data involving breeding adults only. McLain illustrated this differential contribution to total variance in LRS using an example for a population in which some individuals fail to breed, where the contribution to total lifetime reproductive success due to failure to breed is equal to

$$\frac{p(1-p)\overline{\text{LRS}}^2}{p(1-p)\overline{\text{LRS}}^2 + pV(\text{LRS})} = \frac{(1-p)\overline{\text{LRS}}^2}{(1-p)\overline{\text{LRS}}^2 + V(\text{LRS})}$$

As  $p$  decreases, the relative contribution of nonbreeders to total variation in LRS increases.

For the purpose of establishing the argument that the relative strength of sexual selection should be influenced by life-history attributes, McLain equates  $p$  with the proportion of individuals in a population cohort that survive to the age of maturation. Populations that ex-

hibit high mortality in the immature stages will have relatively small contributions to total variance in LRS from variation in breeding success (i.e., the opportunity for sexual selection will be weak), because the greatest contribution to variance in LRS comes from differential survivorship among the early life stages. This assumes that genes responsive to sexual selection are in some way expressed during the immature stage. Using the familiar r-K life-history continuum to advance the basic argument, McLain proposed that relatively r-selected populations under predominantly density-independent regulation should exhibit little response to sexual selection, because most of the failure to breed results from mortality in the immature life stages. In the balance between sexual selection and natural selection, natural selection would have the greatest relative effect in those organisms exhibiting high mortality in large broods. Sexual selection can contribute more toward variance in LRS in K-selected species that have relatively high survivorship at the immature life stage. McLain also noted the possible effect of sexual selection as a directional (diversifying) force, one that may elevate rates of speciation among K-selected species living in density-dependent settings (West-Eberhard 1983).

Two important points about life-history strategies were not covered in McLain's paper: 1) the effects of multiple components of fitness, and 2) the manner in which the unidimensional life-history model shapes corroboration of the theory. Upon initial examination, the first point seems to pose problems for the theory. Yet, consideration of a multidimensional life-history continuum lends new empirical support for the general conclusion that life-history strategies may indeed influence the potential strength of sexual selection.

## Components of fitness

McLain (1991) dealt with fecundity (i.e., clutch size) and survivorship as the sole components of fitness. Here I argue that inclusion of a third axis, timing of reproduction, is essential to comparisons among general life-history strategies. I will not deal with quantitative genetic measures of fitness (Lande 1982, Arnold and Wade 1984), and assume only that a sufficient genetic basis (e.g., heritable phenotypes, appropriate genetic correlations in polygenic systems) and selective environment are required for selection to occur. In life-history theory, the demographic estimate of fitness is usually either  $V_x$ , the reproductive value of an individual or age class (Fisher 1958), or  $r$ , the intrinsic rate of natural increase of a genotype or population (Birch 1948, Cole 1954, Southwood 1988). Each of these estimates contains three essential components: survivorship, fecundity, and the onset and duration of reproductive life. In the case of reproductive value,

$$V_x = m_x + \sum_{t=x+1}^{\omega} \frac{l_t m_t}{l_x} \quad (2)$$

where for a stable population  $m_x$  is age specific fecundity,  $l_x$  is age specific survivorship, and  $\omega$  is the last age class of active reproduction. In this form of the equation, two components of reproductive value are added together: the current investment in offspring ( $m_x$ ) and the expectation of future offspring (residual reproductive value). Reproductive value is therefore equivalent to the lifetime expectation of offspring, and contains survivorship, fecundity, and timing components. The intrinsic rate of population increase can be approximated as

$$r \approx \frac{\ln R_0}{T} \quad (3)$$

where  $R_0$  is the net replacement rate,  $T$  is the mean generation time, and

$$R_0 = \sum l_x m_x, \text{ resulting in } r \approx \frac{\ln \sum l_x m_x}{T} \quad (4)$$

Therefore, the relative rate of genotype or population increase (i.e., relative reproductive success) is directly dependent upon fecundity, timing of reproduction, and survivorship (Southwood et al. 1974, Southwood 1977, 1988, Michod 1979, Roff 1984, Sutherland et al. 1986). In terms of episodic selection, the strength of sexual selection is influenced not only by the negative correlation between fecundity and juvenile survivorship, but also influenced by the age of maturation and the relative length of reproductive life.

## Multidimensional life-history continuum

Given the multivariate nature of life-history strategies and the recognition that the r-K continuum is inadequate for discussions of the implications of life-history configurations, I will reexamine the relative effect of life-history on the strength of sexual selection based on a three-dimensional model of life-history evolution. If two parameters and one dimension are insufficient for understanding the most basic life-history trade-offs, then how many parameters and dimensions are required? Three endpoint life-history strategies have been identified in comparative studies of diverse taxonomic groups, including plants (Grime 1977, 1979), zooplankton (Allan 1976), insects (Southwood 1977, Greenslade 1983), fishes (Kawasaki 1979, Baltz 1984, Winemiller 1989), and reptiles (Tinkle et al. 1970, Dunham and

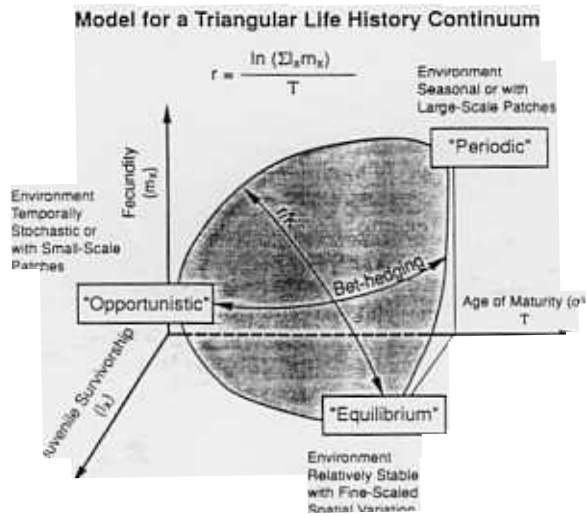


Fig. 1. Model for the adaptive surface of life-history strategies based on fundamental demographic trade-offs and selection in response to different kinds of environmental variation. The "opportunistic strategy" (small  $T$ , small  $m_x$ , small  $l_x$ ) maximizes colonizing capability in environments that change frequently or stochastically on relatively small temporal and spatial scales. A "periodic strategy" (large  $m_x$ , large  $T$ , small  $l_x$ ) is favored in environments having large-scale cyclic or spatial variation. An "equilibrium strategy" (large  $l_x$ , large  $T$ , small  $m_x$ ) is favored in environments with low variation in habitat quality and strong direct and indirect biotic interactions. Curvilinear edges of the surface portray diminishing returns in the bivariate relationships between adult body size and clutch size, adult body size and parental investment/offspring (a correlate of juvenile survivorship), and clutch size and juvenile survivorship.

Miles 1985). A three-dimensional model incorporating the major demographic components of fitness describes an adaptive surface of trade-offs that defines endpoint life-history configurations (Fig. 1). The model implies that trade-offs among life-history parameters (i.e., three demographic parameters and their correlates) are founded in physiological and ecological constraints that ultimately select for genetic correlations (= observed genetic and phylogenetic constraints). Names of the three endpoint strategies are intended to capture the essence of the basic demographic performance and environment of each type of population, and should not be taken to imply, for example, that populations of "equilibrium strategist" persist at constant equilibrium densities.

The optimal reproductive strategy in a given environment is defined by the maximization or minimization of a particular demographic parameter and its relation to trade-offs among other parameters. For example, Smith (1954) and Lewontin (1965) demonstrated how reducing the age of maturation ( $\alpha$ ) most effectively maximizes the intrinsic rate of population increase in density-independent settings (compared with increases in  $m_x$  or  $l_x$ ). The life-history configuration that mini-

mizes  $\alpha$  disallows attainment of large body size and high fecundity. This early-maturation, small-size, low-fecundity tactic could be considered the ideal colonizing or r-strategy. Most microorganisms, especially decomposers and pathogens, exhibit extreme forms of this rapid colonization strategy. This rapid turnover life history comprises the "opportunistic" endpoint among the three endpoint strategies in a triangular surface in three-dimensional space (Fig. 1).

In density-dependent settings, large investments in individual offspring to promote juvenile survivorship is favored at the expense of maximizing  $m_x$  or minimizing  $T$ , or  $\alpha$  (Lack 1954, Goodman 1974). This set of trade-offs describes the traditional K-strategy of large parental investment in individual offspring. Although costly to the parent, the nurturing of offspring presumably gives juveniles greater competitive and predator defense capabilities that improve chances for survival in crowded, resource-limited or dangerous settings. In some cases, stressful environments, like deserts, might select for higher investment in individual offspring (enhancing desiccation resistance, water or nutrient storage) even under density-independent conditions (e.g., stress-tolerant strategy of Grime [1977]). I will refer to the high investment per offspring endpoint as the "equilibrium" strategy.

In seasonal environments, selection favors the production of large numbers of small offspring in pulses that coincide with predictable periods of conditions favorable for growth and survival of immatures (Boyce 1979). The "periodic" life-history strategy also evolves in response to large-scale, yet predictable environmental variation in space as well as time. For example, large batch fecundities in pelagic-spawning marine fishes presumably function to increase the number of eggs hatching in suitable locations in the patchy pelagic environment (Rothschild and DiNardo 1985, Duarte and Alcazar 1989). This strategy of delaying maturation in order to attain large clutches is equivalent to the classical bet-hedging strategy in which adults survive through periods unfavorable for early life stages. Strong cohorts are recruited periodically when early life stages encounter suitable environmental conditions (Murphy 1968, Stearns 1976, Warner and Chesson 1985).

Viewed on a coarse grain, the model describes life-history variation observed in a large variety of organisms (Winemiller 1989, Table 1, Fig. 4), and to some extent, resolves conflicts between earlier unidimensional models of life-history evolution (Stearns 1976, 1977, Southwood 1988). For example the r-K continuum (Pianka 1970) passes through the equilibrium endpoint and the edge connecting the opportunistic and periodic endpoints. A "bet-hedging" axis (Cole 1954, Murphy 1968, Schaffer 1974) would pass through the surface between the opportunistic endpoint and the edge connecting the periodic and equilibrium endpoints. A third axis linking cyclic versus continuous reproduction would pass

Table 1. Examples of basic life-history strategies and associated trends in mating systems and sexual dimorphism based fishes from several major teleost fish families.

Life history strategy	Mating system	Form of sexual dimorphism	Examples
"equilibrium" (late maturity) (small clutches) (high survivorship)	monogamy polygyny, polyandry	male larger and more conspicuous than female	some damselfishes (Pomacentridae)* cichlids (Cichlidae)* sunfishes (Centrarchidae)* darters (Percidae)* pipefishes, seahorses (Syngnathidae) sticklebacks (Gasterosteidae) armored catfishes (Loricariidae) sea catfishes (Ariidae)* some tropical gobies (Gobiidae)* some sculpins (Cottidae)* anabantids (Anabantidae) salmon, trout (Salmonidae)**
"opportunistic" (early maturity) (small clutches) (low survivorship)	polygyny polyandry	male larger or smaller and more conspicuous than female	killifishes (Cyprinodontidae) livebearers (Poeciliidae, Goodeidae) small minnows (Cyprinidae)* small tetras (Characidae)* dwarf cichlids (Cichlidae)* rainbow fishes (Melanotaenidae)*
"periodic" (late maturity) (large clutches) (low survivorship)	polyandry, promiscuity	female often larger than male with little or no coloration difference	the large majority of freshwater, coastal, and marine teleosts [e.g., herrings (Clupeidae), pikes (Esocidae), ciscoes, whitefishes (Salmonidae), bottlenoses (Mormyridae), knifefishes (Apteronotidae, Gymnotidae), suckers (Catostomidae), large tetras (Characidae), large minnows (Cyprinidae), neotropical catfishes (Pimelodidae), old world catfishes (Bagridae, Siluridae) jacks (Carangidae), wrasses (Labridae) snappers (Lutjanidae), mullets (Mugilidae) temperate basses (Percichthyidae), drums (Scianidae), porgies (Sparidae), sea basses (Serranidae), mackerels (Scombridae), billfishes (Istiophoridae), flatfishes (Bothidae, Pleuronectidae)]

\* Other species within the family exhibit one or more alternative life history strategies.

\*\* High investment in individual offspring is in the form of placement of massive eggs in special habitats rather than extensive brood-tending behavior.

through the surface between the periodic endpoint and the opportunistic/equilibrium edge.

### Sexual selection and life-history strategies

The classical K-strategy (delayed maturation, iteroparity, and parental investment in relatively few offspring) largely corresponds with the equilibrium strategy as described in Fig. 1. Given long lifespans and high survivorship in both immature and adult stages, equilibrium strategists should have a high potential for mating success to contribute a large proportion of variance in LRS. What about the relative effectiveness of sexual selection on the opportunistic strategy (small colonizing organisms with rapid maturation and rapid population turnover) and periodic strategy (larger species with delayed

maturation, large clutches and pulsed reproduction that exploits a regularly varying environment)? Successful individuals in colonizing populations with rapid turnover are dependent upon successful reproduction during a lifespan that, in all likelihood, will be short due either to an unstable, harsh, or dangerous environment. Given this premium on all-out reproduction (i.e., rapid maturation and large reproductive effort via production of multiple small clutches over short intervals), variation associated with mate choice and competition for mates should encompass a large fraction of  $V(LRS)$  relative to variation in survivorship of immature age classes. Conversely, given that a huge amount of variation in  $l_x$  is possible during the immature stages of highly-fecund periodic strategists, only a tiny fraction of total variance in LRS would be represented by differential mating success.

It is important to note that huge variation in juvenile

survivorship of highly-fecund organisms would swamp out the potential influence of variation in mating success only in the case in which the variance in immature survivorship is, at least to some small extent, nonrandom. This nonrandom variation in immature survival rates would not have to be consistently directional or stabilizing in order to override any potential influence of differential matings. If variation in juvenile survivorship is entirely and consistently random, the small variance component of LRS associated with sexual selection could result in the evolution of sexually dimorphic characteristics. The situation would be analogous to the gradual evolution of morphological feeding specializations in the face of periodic density-independent disturbances. Selection associated with resource states or competition can be consistently directional in the long term, even though it is interrupted by episodes of catastrophic mortality caused by severe climatic conditions.

### Teleost fishes

A brief review of flashy sexually dimorphic traits and life-history patterns in fishes confirms the hypothesis that sexual selection is weak or absent in highly-fecund, periodic strategists. As a group, fishes span a very wide range of life-history strategies (Itô 1978, Kawasaki 1979, Mahon 1984, Winemiller 1989). Equilibrium strategists are prevalent in several tropical freshwater and marine families. For example, most fishes of the tropical Cichlidae exhibit several months of biparental care for relatively small broods. In some instances, just a few offspring are protected inside the mouth of one or the other parental sex (e.g., neotropical *Geophagus* spp., African haplochromines, *Oreochromis* spp., *Sarotherodon* spp.); a tactic also seen in the marine catfishes (Ariidae). Aggressive nest defense is common in several major teleost families, and pouch brooding and other kinds of external bearing are seen in some others (e.g., Syngnathidae). Rapidly maturing, opportunistic strategists are found among the small killifishes (Aplocheilidae, Cyprinodontidae), neotropical livebearers (Poeciliidae, Goodeidae), silversides (Atherinidae), and anchovies (Engraulidae). Yet clearly, the large majority of teleost fishes would be classified as relative periodic strategists (i.e., small eggs and larvae, large batch fecundities, and fairly synchronized reproductive seasons).

Table 1 lists examples of life-history strategies, mating systems, and the relative development of conspicuous, sexually-dimorphic traits in several major teleost taxa. Construction of Table 1 was based on information derived from my field research (Winemiller 1989, 1991, Winemiller and Taphorn 1989) and review of the diverse fish life-history literature (readers can consult the following compendia: Breder and Rosen 1966, Hart 1973, Scott and Crossman 1973, Thresher 1984). Even though

Table 1 does not represent an exhaustive survey, several trends that bear on the sexual selection/life-history hypothesis seem obvious. Although teleosts span all three life-history strategies, species within a given family tend to be centered around only one or two strategic endpoints. Obviously the position of a species within a life-history continuum is relative and scale-dependent, so here I am referring only to comparisons made across a broad spectrum of teleostean diversity.

Mating system seems to be strongly associated with life-history strategy. Polygyny is widespread among equilibrium and opportunistic species and promiscuity and polyandry are common among broadcast-spawning, periodic strategists. In addition, many of the relative equilibrium strategists exhibit monogamous matings, at least on an annual or serial basis. Many of the opportunistic species, killifishes and livebearers in particular, exhibit serial polyandry in addition to polygyny. I would be hesitant to classify the latter cases as promiscuity due to the selective nature of many of these matings (i.e., males mating with multiple females and females sequentially choosing several males, Kodric-Brown 1985).

Conspicuous sexually dimorphic traits that likely result from sexual selection are numerous among equilibrium and opportunistic strategists, but effectively absent in periodic strategists. Numerous examples of striking color patterns and elaborate fin development among males of many small tropical species are well known by aquarists (e.g., unique and bright coloration, nuchal humps, elongate fins). Yet, the apparent absence of flashy male characters among highly-fecund, periodic strategists is particularly striking, given that they comprise the largest life-history grouping among teleosts. This assessment agrees with Chandler and Cabana's (1991) finding that adult size and age of maturity are negatively correlated with sexual dichromatism in North America freshwater fishes. Large fishes with clutches numbering in the tens or hundreds of thousands are sexually monomorphic. Among high-fecundity fishes, marked sexual dichromatism seems to be found only in species showing protogynous sequential hermaphroditism (e.g., tropical parrotfishes [Scaridae] and wrasses [Labridae]). Sexual dichromatism in these sex-switching species communicates both gender and the social status of individuals on reef territories. Sexual selection in protogynous hermaphrodites can permit a small difference in size or age to confer a massive difference in fertility (Warner et al. 1975). In contrast to highly-fecund (periodic strategy) fishes, equilibrium and small opportunistic strategists exhibit fairly widespread incidence of sexual dichromatism (Table 1). Where strong directional selection favors crypsis or special warning signals, monomorphism is encountered in these groups as well.

As a further test of the association between life-history strategy and sexual selection, I looked at the relationship between relative sexual dichromatism and body size, clutch size, and egg size in North American percid

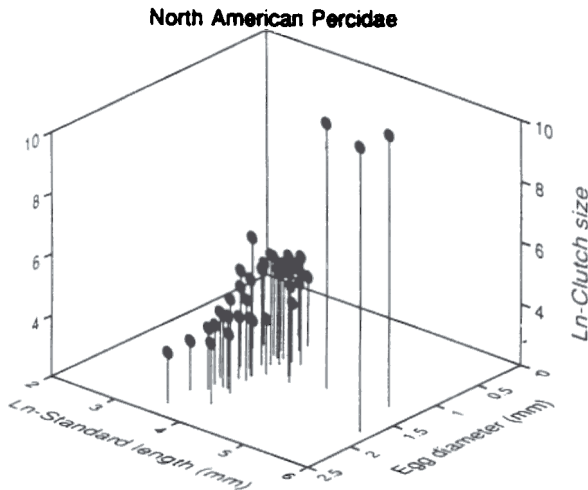


Fig. 2. Plot of 40 North American percid fishes on three life-history axes: ln-average standard length (a correlate of maturation rate and population turn-over time), ln-average clutch size, and egg diameter (a positive correlate of investment/progeny and juvenile survivorship).

fishes. Relative sexual dichromatism was estimated from color photographs of male and female darters in Page (1983) using a slight variation of the method of Ward (1988). In addition to skin pigmentation, I considered sexual differences in fin pigmentation of fishes in breeding condition. Average lengths (SL), average clutch sizes, and average egg diameters were obtained from Paine (1990) and Carlander (in press). A 3-D plot

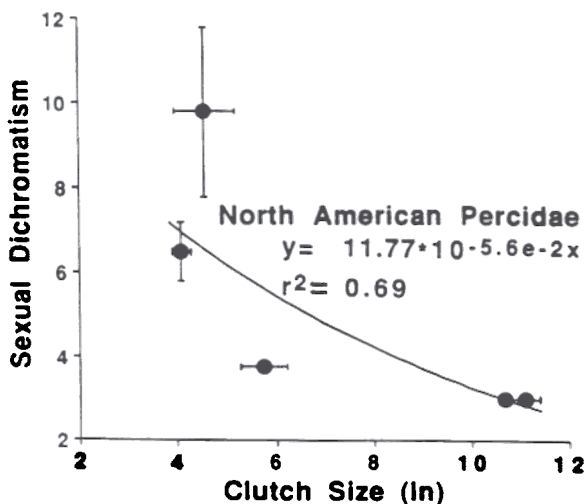


Fig. 3. Relationship between average clutch size and sexual dichromatism among genera of North American Percidae (No. of species: *Ammocrypta* = 2, *Etheostoma* = 31, *Perca* = 1, *Percina* = 4, *Stizostedion* = 2). A value of 3 on the y-axis indicates no sexual difference, points are genus means, and error bars are  $\pm 1$  SD.

of ln-clutch size by ln-adult length by egg size (Fig. 2) produces a series of points that approximate a part of the life-history adaptive surface in Fig. 1. Here egg size (relative investment per progeny) is taken as a surrogate for juvenile survivorship, and average adult length serves as a surrogate for average generation time. In North American darters, ln-body length and ln-clutch size are negatively associated with relative sexual dichromatism, both at the level of species (exponential model: length  $r^2 = 0.30$ , clutch  $r^2 = 0.46$ ) and genus (exponential model: length  $r^2 = 0.51$ , clutch in Fig. 3). Other families that display a wide range of life-history strategies show the same trend: the largest species with the largest clutches show the least sexual dichromatism (e.g., Centrarchidae, Cyprinidae, Characidae). Given the consistency of this pattern between higher taxa, it seems doubtful that the trend within a given phylogenetic clade arises solely as an historical accident during character divergence. Quantitative tests of the hypothesis should be feasible for other fish families and other higher animal taxa that exhibit large variation in life-history strategies.

Patterns of sexual size dimorphism also seem to show some degree of correlation with life-history strategies. Among equilibrium species, males tend to be the larger of the two sexes. For many substrate nesting species, large male size is probably associated with the successful acquisition of limited optimal nest sites (Baylis 1981). Some anemone fishes (Pomacentridae) exhibit social control of protogynous sex changes in which the largest and most dominant individual within the group's territory (territory = anemone) becomes the male (Fricke 1979). Among opportunistic species, males may be either larger and flashier (e.g., annual killifishes [Cyprinodontidae] or smaller and flashier (guppies [Poeciliidae]) than females. Again, the nature of size differences may relate to the social system and competition among males for the acquisition of high quality habitats. For example, male killifishes tend to be extremely territorial, and male guppies are nonterritorial. Among periodic strategists, the female is generally the larger of the two sexes, or less commonly there is little apparent size difference in growth rates of the sexes. It is noteworthy that most of the world's important commercial fish stocks tend to be associated with the periodic life-history strategy.

### Other taxonomic groups

Fig. 4 illustrates the variation in basic life-history strategies exhibited by other higher taxonomic groups. Within each major grouping, organisms can be subgrouped into relative life-history strategies based on their location on the adaptive surface. These subgroupings should be viewed only in a relative sense within a broad comparative framework (e.g., Allan 1976, Whit-

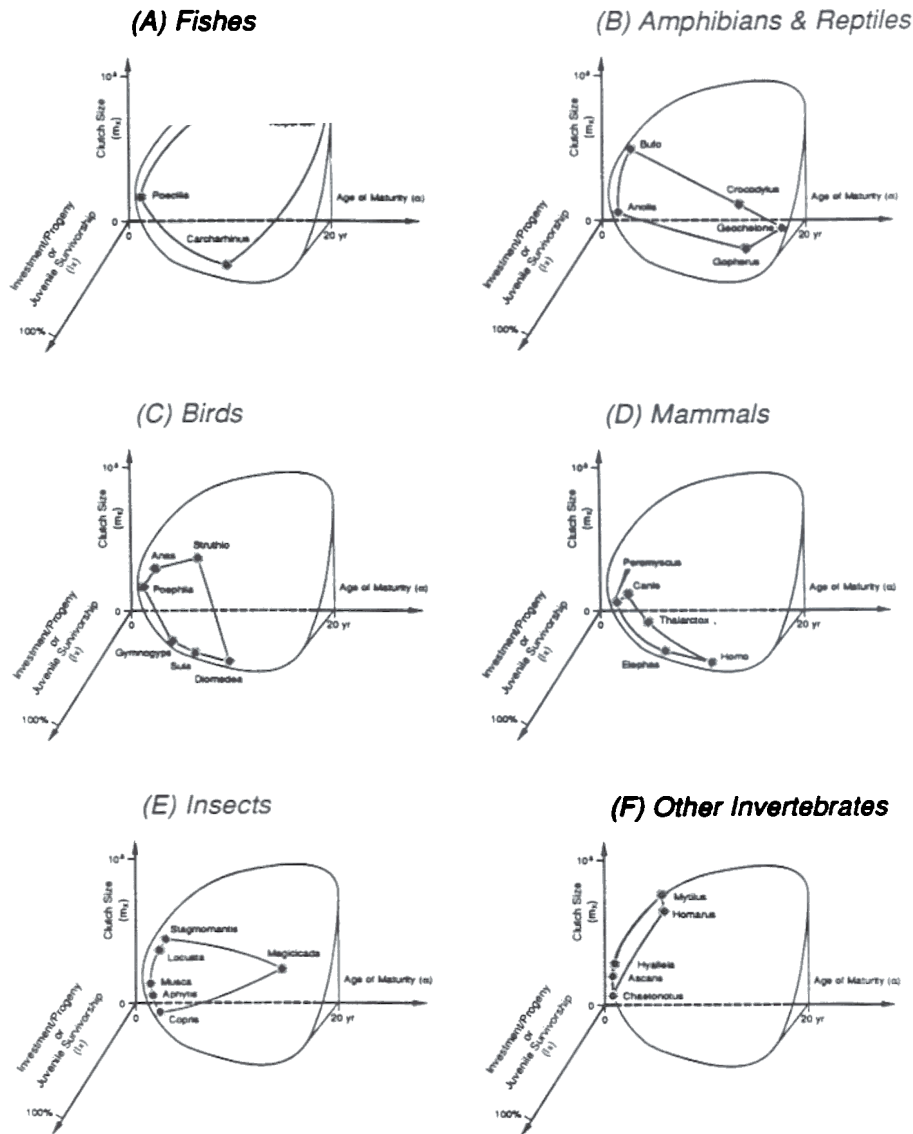


Fig. 4. Relative locations of major groupings of animals on an adaptive surface of basic life-history strategies: (A) fishes: *Poecilia reticulata* [guppy], *Mola mola* [ocean sunfish], *Acipenser fulvescens* [lake sturgeon], *Carcharhinus limbatus* [blacktip shark]; (B) reptiles and amphibians: *Anolis limifrons* [tropical lizard], *Bufo americanus* [toad], *Crocodylus niloticus* [crocodile], *Gopherus agassizi* [desert tortoise], *Geochelone gigantea* [giant tortoise]; (C) birds: *Poephila guttata* [zebra finch], *Anas platyrhynchos* [duck], *Struthio camelus* [ostrich], *Gymnogyps californicus* [condor], *Diomedea exulans* [albatross]; (D) mammals: *Peromyscus truei* [mouse], *Canis latrans* [coyote], *Thalarctos maritimus* [polar bear], *Homo sapiens* [human], *Elephas maximus* [elephant]; (E) insects: *Aphis chrysomphali* [aphid], *Musca domestica* [housefly], *Locusta migratoroides* [locust], *Magicicada septendecula* [cicada], *Stigmomantis carolina* [mantis], *Copris acutidens* [dung beetle]; (F) other invertebrates: *Chaetoniou tachyneusticus* [rotifer], *Hyallela azteca* [amphipod], *Ascaris lumbricoides* [nematode], *Acanthaster planci* [starfish], *Mytilus edulis* [muscle], *Taenia pisiformis* [tapeworm], *Homarus americanus* [lobster]. Estimates for age of maturation and clutch size came from a variety of literature sources (e.g., Lack 1968, Eisenberg 1981), and juvenile survivorship was only roughly approximated in terms of species ordinations based on relative parental investment (in terms of matter, energy, parental care tactics) per individual progeny.

taker and Goodman 1979, Dunham and Miles 1985). Within most taxonomic groups, species marked by flashy sexually dimorphic characteristics and size dimorphisms are easily recognizable in the equilibrium

region of the surface (delayed maturation, small clutches, high juvenile survivorship). The following are just a few examples from the animal kingdom (I defer discussion of female choice in plants to the botanical

experts): bright coloration and large size in male dragonflies, body size and longer dorsal spines in male iguanas, sexually dimorphic coloration in the poisonous boomslang snake, striking coloration and plumage in male peacocks and many other birds, and larger body size and bright facial coloration in the male mandrill baboon. Yet the apparent absence of conspicuous sexually dimorphic characteristics is also notable in many equilibrium type species that invest a large amount of parental care in small numbers of offspring (e.g., viviparous sharks, eagles, canids). Apparently strong natural selection overrides sexual selection in many equilibrium-type organisms. The reasons why sexual selection produces dimorphic phenotypes frequently within some equilibrium-dominated clades (birds) but only rarely in others (snakes) deserves attention.

Strong sexual dimorphisms are also common but not universal among opportunistic strategists in Fig. 4 (early maturation, small clutches, low juvenile survivorship). For example, males are flashier and larger in several small opportunistic species of insects (enlarged rostrum in some weevils and other small beetles), lizards (colorful dewlaps in *Anolis* spp.), and birds (plumage coloration in small finches and sparrows). With the exception of size differences, little obvious sexual dimorphism is reported among rapidly maturing species of crustacea, amphibians, and rodents. Again, directional selection from predation and other ecological factors probably inhibits sexual selection in monomorphic opportunistic species.

As seen among teleost fishes, no clear examples of sexual dimorphism in coloration or morphological structures used for mate attraction come to mind for the periodic strategists in Fig. 4 (delayed maturation, large clutches, low juvenile survivorship). Highly-fecund insects, crustacea, amphibians, and reptiles may show size dimorphisms (females larger), but no distinctive sexual dichromatism. Some highly fecund insects and anurans (amphibians) are sexually dimorphic in their acoustical signals, just as certain electrical fishes (tropical freshwater mormyriforms and gymnotiforms) show marked differences in the signals produced by the mature sexes (Kramer 1990). According to Kirkpatrick and Ryan (1991), sexual dimorphism in sensory signals of lekking species probably arise from direct selection on female fitness (via pleiotropy) through exploitation of preexisting sensory biases.

## Conclusions

A three-endpoint, life-history continuum provides a simple, yet comprehensive model for testing the idea that life-history strategies should influence the strength of sexual selection. Fitness is influenced by three demographic components: survivorship, fecundity, and the timing of reproductive events (early versus delayed

effort). Each of the endpoint strategies is defined by the optimization of one component at the expense of the other two. A preliminary review of life-history strategies in teleost fishes reveals that flashy male traits are common among equilibrium and opportunistic-type species. In confirmation of McLain's general hypothesis, fishes exhibiting the strategy of periodic production of large clutches seem to show little, if any, evidence of sexually-selected male traits. Protogynous hermaphrodites appear to represent the sole exception to this rule. A cursory review of other large taxonomic groups seems to follow the fish patterns. The idea that the strength of sexual selection should be influenced by life history is closely linked to the hypothesis that the sexually selected sex will be the one with the fastest reproductive rate (Clutton-Brock and Vincent 1991). It is noteworthy that all 28 sexually-dimorphic species reviewed by Clutton-Brock and Vincent (1991) exhibit parental care and relatively small clutch sizes (i.e., a relative equilibrium strategy).

Following West-Eberhard's (1983) suggestion that sexual selection is diversifying, McLain (1991) proposed that speciation via sexual selection will be greater among K-selected species in density-dependent settings. Indeed, well-known examples of species flocks involve opportunistic and equilibrium-type fishes distinguished by their sexually dimorphic coloration patterns (e.g., killifishes of Lake Titicaca [Peru], small cyprinids of Lake Lanao [Phillipines], cichlids of the African rift lakes). However, other factors may lead to higher rates of speciation in opportunistic species relative to equilibrium species. Short-lived species with rapid population turnover times have the greatest potential for rapid evolution and divergence of lineages. Moreover, opportunistic species tend to be associated with habitats that are frequently disturbed and fragmented. Marzluff and Dial (1991) recently showed a strong correlation between biotic diversity and traits associated with the opportunistic life-history strategy (e.g., rapid maturation and high  $r$ ). They suggest that traits associated with rapid colonizing capability both enhance rates of speciation and reduce the probability of extinctions. Apparently, diversity is enhanced in opportunistic species by the dual action of large capacity for population growth and responsiveness to sexual selection. Diversity in equilibrium species might be promoted by sexual selection, but inhibited by low inherent capacity for rapid population growth in response to environmental disturbances. Sexual selection does not appear to be a significant force promoting diversity in periodic strategists. Potentially, the effect of large fecundity on the intrinsic rate of increase could be massive if periodic or unusual environmental conditions were to favor high survivorship among juveniles. In addition, diversity in many periodic strategists could be inhibited by the great dispersal capabilities of migratory adults and small, vagile propagules.

Finally, the observation that massive, but entirely



random mortality at the immature stages should not influence the strength of sexual selection is important, because it carries overtones for applied research. Either of two factors would inhibit sexual selection in species exhibiting the periodic life-history strategy: 1) nonrandom variation in differential mortality among immature age classes, and 2) a lack of consistent asymmetries in the variation in mating success. The ample evidence of sexually selected characters among taxa associated with other life-history strategies makes the second alternative highly unlikely. The virtual absence of flashy male traits in periodic fishes seems to confirm a popular contention among fisheries scientists; that variation in mortality rates during the pelagic, early life stages of highly-fecund species is nonrandom (e.g., hypotheses of size-dependent mortality in larval fishes).

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