

Chapter 5

**SOCIAL STRUCTURE AND INDIVIDUAL
ONTOGENIES: PROBLEMS OF DESCRIPTION,
MECHANISM, AND EVOLUTION**

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I. ABSTRACT

An old problem in the study of societies is the relationship between social structure and the development of individuals. Societies generally have a more or less stable distribution of individuals among social positions in spite of the passage of successive generations of individuals. For biologists, the problem of the relationships between individual and society has three aspects: the quantitative description of individuals' movements through successive social positions; the mechanisms that regulate this movement; and the evolution of these regulatory mechanisms.

The concept of "ontogenetic trajectories" can serve as a basis for describing the movements of individuals through social positions. Actual measurements of the age-dependent rates of transitions of individuals from one social position to another should soon permit the first relatively complete descriptions of complex animal societies. Ontogenetic trajectories raise questions about the mechanisms that generate stable distributions of individuals among social positions. In some cases, there is evidence of feedback control in the form of inhibition by individuals in a later social position on the development of individuals in earlier positions. In other cases, stable social structure might result from relatively constant demographic conditions and developmental schedules.

The evolution of ontogenetic trajectories, in particular ones that involve substantial deferment of successful reproduction, is related to the

evolution of life-history strategies. Several recurring forms of social structure in birds and mammals, in particular polygyny and stable groups of cooperating adults with one reproductive pair, raise similar questions about the evolution of maturational controls that result in ontogenetic trajectories with delayed reproduction. Some simple calculations can show that the evolution of delayed reproduction depends on the consequences of early reproduction for subsequent survival and fecundity. In the end, explanations for the evolution of polygyny and cooperative groups will need to incorporate ecological explanations for the adaptedness of ontogenies with delayed reproduction, rather than present delayed reproduction as a secondary consequence of the social structure.

II. INTRODUCTION

In the first half of this century, those biologists who turned their attentions to animal societies often adopted simple analogies for the relationship of society and individual. Students of social insects likened the societies of ants, bees, and wasps to individual organisms. Indeed, the analogy between society and organism, an idea with a long history, was particularly captivating for biologists during the second quarter of the century (see Comte, 1830; Mills, 1843; Wheeler, 1926; Canon, 1932; Clements, 1935; Emerson, 1939; Jennings, 1942). There undoubtedly exist certain fundamental parallels in the relationships between any two levels of biological organization. Understanding how cells interact to regulate an organism's internal homeostasis has some similarities, at least in form if not content, to understanding how individual animals interact to regulate a population's social structure. Nevertheless, there are some crucial differences, which few biologists fully perceived until recently.

Already in 1932, Haldane had recognized a key problem in the evolution of individuals' relationships in a society. How could natural selection favor the genes of individuals, such as the sterile workers in the social insects, that sacrificed their own reproduction and increased the reproduction of others? This question of the evolution of altruism, neglected for three decades, was to provide a major impetus for the recent development of a biology of animal societies.

Intensive biological investigation of the relationships of individuals and society began around 1930 with Allee's (1942) studies of dominance hierarchies and Schneirla's (1971) studies of army ants. Both focused on the behavioral and physiological mechanisms that regulate social structure. Allee and his students investigated in detail the physiological and experiential

social structure with particular populations or species of animals. The persistence of social structure in spite of a continual turnover of individuals has prompted such concepts in sociology as a collective conscience or norms of behavior. Although these concepts are not useful in analyzing animal societies, the question remains a legitimate one: how do successive generations of individuals come to adopt such similar social organizations?

A biologist immediately sees that this question presents a host of problems in the genetics, physiology, and development of behavior. Although many relevant aspects of these problems have received attention, biologists have yet to put this information together in a coherent explanation of the mechanisms that control the relationships between individual behavior and social structure for any species. During the spate of research since 1960 on the evolution of animal societies, there has been no comparable attempt to develop a systematic framework for understanding the mechanisms of animal societies, the physiological and behavioral controls of individuals' ontogenies that generate a persistent social structure.

Before analyzing the mechanisms that regulate the social structure of a population, we need a framework for describing the flow of individuals in time through positions in the society. By analogy, in physics a study of kinematics, a quantitative description of the movements of the components of a system without regard to the forces involved, might precede a study of dynamics. To describe the flow of individuals in time through a more or less persistent social structure, I have found helpful the concept of "ontogenetic trajectories" of individuals through social positions in a society. A trajectory is an appropriate analogy for the movement of individuals through positions in a society. The development of any individual depends on its initial genetic endowment and its exposure to environmental and social influences during the course of its life, just as the movement of a projectile depends both on its initial conditions and its continuing interaction with the medium through which it passes.

Biologists attempting to understand the relationship between individuals and societies thus confront three categories of problems: description, mechanism, and evolution. The following pages develop the concept of ontogenetic trajectories first as a tool for describing the structure of a society, then as a basis for analyzing the behavioral and physiological mechanisms that regulate social structure, and finally as a perspective on animal societies that raises some pervasive evolutionary questions.

III. ONTOGENETIC TRAJECTORIES

Although the development of behavior has long been a major emphasis in psychology and ethology, most of this work has focused on the develop-

determinants of dominance, but they also took a clear interest in the effects of dominance on the reproduction and survival of individuals (Allee, 1942). They concluded that the greater fecundity and physiological condition of dominant animals indicated greater evolutionary fitness. Thus, prior to 1950, biologists had taken the first steps in understanding the behavioral and physiological control of social structure and had identified some central problems in the evolution of social behavior.

During this period, sociologists who wrestled with the relationships between individuals and society had little discernible influence on biology. Some schools of sociology emphasized the effects of society on the behavior and development of individuals. Durkheim (1972) in particular elaborated the view that every society has a collective conscience that persists across successive generations of individuals and molds the behavior of each generation. Social psychologists, following Mead (1934) and Merton (1949), emphasized that individuals appraise their actions in the light of the expectations of others. Other schools of sociology gave more emphasis to the effects of individual motivation on social behavior. Parsons (1951), for instance, attempted to reconcile psychological and sociological approaches to human behavior by developing a conceptual scheme in which human action is controlled by interacting social, cultural and motivational influences.

Perhaps one reason that sociology and biology have found so little common ground stems from a procedural difficulty. Sociologists share, in spite of their differences, a common emphasis on a system of norms or expectations held in common by sets of individuals in a society. The concept of norms of behavior is not easily accommodated in studies of animal societies. Sociologists determine the norms or expectations of the members of a society by means of verbal interaction with their subjects, or in some cases introspection — techniques that have no application in the study of animal societies. Even the recent advances in verbal communication with apes raise no immediate hope of verbal interactions with apes in their naturally occurring societies.

Nevertheless, the basic problem, if not the technique, that has occupied sociologists seems applicable to animal societies. A characteristic of all societies is a recognizable structure that persists with relative constancy in spite of the passage of succeeding generations of individuals. At any one time, the individuals in a particular population exhibit characteristic differences in behavior, often identifiable as more or less discrete behavioral categories. The basic characteristics of the behavior of individuals in these categories and the proportions of the population or the absolute numbers of individuals in each category often remain relatively constant with time. This structure of a society, in spite of some important variation in time and space, remains constant enough that we can associate characteristics of

ment of behavior in immature animals. The concept of ontogenetic trajectories can serve to emphasize the important changes in the social positions of individuals throughout their lives.

Changes in the social behavior of individuals are probably best understood in social insects. The most thoroughly documented example is the worker honeybee. By following marked individuals, an observer finds not only a general change from participation in duties within the hive to foraging outside the hive, but also more subtle changes in the kinds of duties that occupy bees within the hive (Lindauer, 1952; Wilson, 1971).

This example probably provides the only case so far in which ontogenetic trajectories have been determined directly, by observing marked individuals throughout their lives. Indirect determinations of ontogenetic trajectories rely on observations of individuals changing from any one social position to others. Individuals' possible ontogenetic trajectories are then reconstructed from these observations of changes from one social position to the next. This sort of reconstruction amounts to the use of a first-order Markov process to estimate sequences of behavior. In this case each state is a social position, and the observer assumes that transitions of individuals from one social position to another occur independently of their previous histories. This indirect analysis of ontogenetic trajectories has been applied extensively to the castes in termite societies.

The movement of individuals through different castes in termite societies illustrates some of the features of ontogenetic trajectories (see Wilson, 1971; McMahan, 1979). In the primitive families of termites, the changes of individuals from one caste to another are extremely complex. Often colonies include individuals with characteristics intermediate between the definitive characters of different castes. Furthermore, individuals have great developmental flexibility. At any age after the third or fourth instar, individuals can molt into soldiers or reproductives and even molt retrogressively (Miller, 1969).

In contrast, most of the higher termites (Termitidae) have relatively well-defined ontogenetic trajectories of individuals through different castes (Noirot, 1969). Often the trajectories permit no branching or regression after the first instar. Particularly interesting, however, are trajectories that branch into two discrete paths (Fig. 1).

Although the paths by which individuals develop are now well established for a variety of social insects, much less is known about the time that individuals spend in successive social positions or castes. Estimates of these durations and their variances require observations of marked individuals. When individuals cannot be followed throughout their lifetimes, an observer can follow samples of marked individuals in each identifiable social position. A map of the possible ontogenetic trajectories of individuals through social positions in combination with estimates of the rates at which

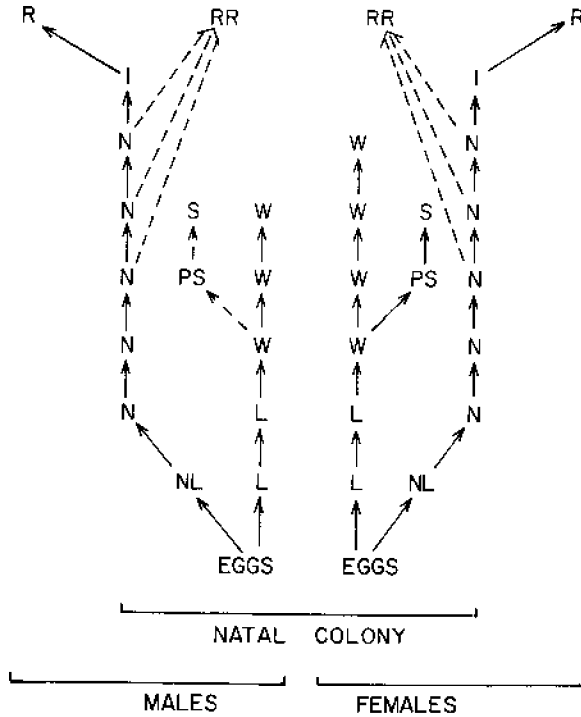


Fig. 1. Ontogenetic trajectories of a higher termite (*Microcerotermes*, Termitidae). The vertical scale indicates successive instars, not actual time; the stages vary in duration. Developmental paths for reproductive and nonreproductive individuals divide at an early age, possibly before the eggs hatch. Larvae are indistinguishable by external morphology in the first stage, but before the first molt they have already divided into two groups: larvae (NL) destined to develop into nymphs (N), imagoes (I), and reproductives that found new colonies (R) or replacement reproductives in the natal colony (RR); and larvae (L) destined to develop into workers (W) and soldiers (S). In this genus, female nonreproductives are larger than males, a difference that becomes evident among second-stage larvae. Such differences in size often correlate with behavioral differences. Soldiers develop primarily from female workers, rarely from males. In other genera of higher termites, ontogenetic trajectories of nonreproductives take a variety of patterns, but males and females usually have substantial differences. In the families of lower termites, developmental pathways are not so fixed. In particular, the early division between reproductive and nonreproductive lines does not occur and there are no differences between the sexes in ontogenetic trajectories. Modified after Noirot (1969).

individuals change from one position to the next (or the residence times of individuals in each social position), the mortality rates of individuals in each social position, and the recruitment of individuals to the population provide the information for a complete kinematic model of a society.

Among vertebrates most species have societies with much less complex structure than those of termites. In many cases, societies seem to have only a few identifiable social positions for mature animals. Consider a territorial passerine bird. During the breeding season, we might recognize territorial and nonterritorial males and mated and unmated females: two social positions for all individuals of each sex.

Of course the structural complexity of a society depends on how finely we classify social positions. We could recognize several categories of behavior for a territorial male bird, for instance feeding, courting females, and defending his territory; then we could analyze the individual's transitions from one to another of these categories of behavior on a finer timescale than we could analyze longer-term changes from nonterritorial to territorial status. In analyzing social structure of vertebrates, I will use the term social position to refer to patterns in individuals' social behavior that normally persist over periods of days at least, in order to distinguish these patterns from those that are recognizable over periods of minutes or hours.

The term social "role" has in the past applied to both of these time scales. "Role" has an additional ambiguity as a result of a somewhat different connotation in much sociological literature. There it often means the norms or expectations for an individual's actions, while "position" usually refers to more objective criteria for differentiating individuals, such as an individual's age, title, genealogical relationships, or actions. Sociologists do not always draw this distinction, but when they do, the term "position" is more consistently used for the objective criteria that differentiate individuals (Sarbin and Allen, 1969).

The different species of grouse (Tetraonidae) provide some instructive contrasts in complexity of social structure. According to the thorough studies of red grouse (*Lagopus lagopus*), males older than about six months fall into only two categories of social behavior, territorial and nonterritorial birds. Males barely four months old seem equal to older males in obtaining territories and mates (Watson and Moss, 1972). Thus the red grouse fits the pattern for a simple avian society with two social positions for mature individuals of each sex. In contrast, among those species in which the males congregate at leks, all full-grown males are not equivalent in their access to choice territories. Those males with territories near the center of a lek copulate much more frequently with visiting females than do males with peripheral territories or nonterritorial males (reviewed by Wiley, 1973).

Just in the last decade evidence has accumulated that males usually acquire central territories after first establishing peripheral territories on a lek and then moving their positions toward the center. I inferred this centripetal movement of males on leks of sage grouse (*Centrocercus urophasianus*) by the indirect means of observing the reoccupation of territorial vacancies (Wiley,

1973). Invariably a vacancy was occupied by one or more neighboring males who moved their territories toward the center of the lek. This sort of indirect evidence is much like that used to deduce the trajectories of termites through castes. More direct evidence comes from studies of marked populations. Both for sharp-tailed grouse and black grouse, males on the periphery of a lek have moved subsequently into central positions (Kruijt *et al.*, 1972; de Vos, 1979; Rippin and Boag, 1974). No study yet has marked enough birds and followed them long enough to establish the means and variation for the transition rates between positions on a lek or the residence times in different positions on a lek.

It seems possible that the males of many polygynous species have ontogenetic trajectories that involve a sequence of social positions leading to a position that permits high fecundity, in essence a queue for access to opportunities for reproduction. The lek-forming grouse provide an example in which such ontogenetic trajectories correspond with actual movements of individuals' territories in space. Probably in all polygynous birds and mammals, males begin successful reproduction on average at later ages than do females. Among antelope, males acquire territories and opportunities to copulate with females several years after females begin reproduction (see, e.g., Spinage, 1969; Jarman and Jarman, 1974; Gosling, 1974). Male elephant seals (*Mirounga angustirostris*) continue to grow for approximately twice as many years as do females. Although only the larger, and consequently older, males become harem masters, males begin to frequent breeding grounds regularly at younger ages (LeBoeuf, 1974). One wonders whether queuing might not also occur in these species, in the sense that a male acquires a position as a successful breeder through a prolonged and gradual process of exploiting small advantages among males in the immediate area in which he eventually succeeds to full reproductive status.

Among some primates also, older males tend to dominate younger ones, and more dominant males tend to copulate most frequently, although there is considerable variation among species and even among populations in both of these generalizations (Hausfater, 1975; Wade, 1978; Packer, 1979). Primates, owing to their relatively long lives, have been difficult subjects for descriptions for social kinematics. Until very recently, most studies of primate societies in the field reported only isolated anecdotes of mature individuals that changed social positions. The histories of dominance and reproductive success of males throughout their lives have been especially difficult to obtain. The initiation in the last two decades of long-term studies of primates in the field should remedy this situation soon.

Another complex form of vertebrate society, stable groups of cooperating adults, also invites an analysis of ontogenetic trajectories. Several mammalian carnivores, in particular the wolf (*Canis lupus*), the hunting dog (*Lycaon pictus*), and a few viverrids, share some striking

features of social behavior with certain birds in more than a dozen phylogenetic families (Brown, 1978; Emlen, 1978; Rasa, 1977; Frame and Frame, 1976; Mech, 1970). In these species, adults associate in stable groups that usually average five to eight. The members of a group cooperate in defending a shared territory. Usually only one male and female in each group breeds, although the other members of the group help to feed the young. These groups thus consist of two clearly different social positions for adults, reproductives and nonreproductives. For the study of ontogenetic trajectories, the birds have some clear advantages over the mammals with this sort of social organization. Because large numbers of birds can often be marked individually and then be subject to a reliable census, information accumulates more rapidly on the transition rates and residence times of individuals in different social positions.

The South American stripe-backed wren (*Campylorhynchus nuchalis*) presents optimal conditions for a complete documentation of the ontogenetic trajectories in a complex vertebrate society. The members of a group of stripe-backed wrens all sleep each night in the same enclosed nest, a habit that makes it possible to take a complete census of the population by counting the birds as they leave and enter their nests. In addition, by decoying the birds with playbacks of tape-recorded vocalizations, one can capture and mark individually almost every individual in a population. Rabenold now has more than 150 individuals in 25 contiguous territories under study (see Wiley and Wiley, 1977; Wiley, 1978; Rabenold and Christensen, 1979).

To construct a kinematic model of this society, we recognize three social positions: dependent juveniles, auxiliary (nonreproductive) members, and principal (reproductive) members of groups. The preliminary data are sufficient to give a general picture of the model; Rabenold will soon have estimates of the transition rates between social positions and residence times for each sex in each social position. The picture that emerges is a remarkably general pattern of social kinematics for species with stable groups in which one male and female reproduce and other adults help (Fig. 2). A sex difference in ontogenetic trajectories applies to hunting dogs as well as the group-territorial birds: females become reproductives primarily through emigration from their natal groups, whereas males become reproductives within their natal groups (Zahavi, 1974; Frame and Frame, 1976; Woolfenden and Fitzpatrick, 1978). For males, the process of ascending to reproductive status amounts to a form of queuing. Even for females, at least in stripe-backed wrens, there is an element of queuing in succession to reproductive status, since a vacancy for a female breeder is usually filled by a female from an immediately adjacent territory. In both sexes, it pays to have lived in the immediate area when an individual tries to succeed to a reproductive position.

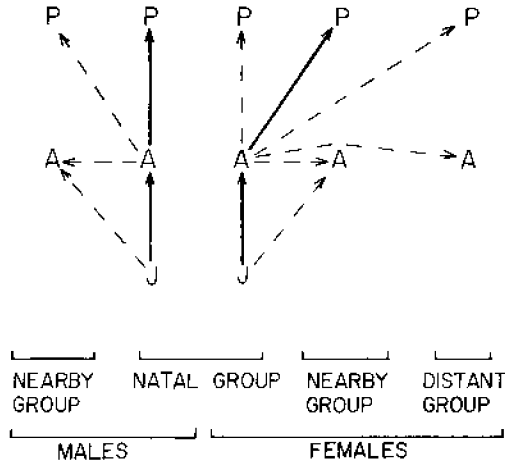


Fig. 2. Ontogenetic trajectories of stripe-backed wrens (*Campylorhynchus nuchalis*, Troglodytidae). The vertical scale indicates successive social positions in stable social groups; the stages vary in duration. Most juveniles (J) join their natal groups as nonreproductive adults or auxiliaries (A). A female usually succeeds to a reproductive, or principal (P), position by occupying a vacancy created by the disappearance of a principal female in a nearby group. A male usually becomes a principal member of a group by succession within the natal group. Dashed lines indicate infrequent transitions between social positions. Based on studies by K. Rabenold, C. Christensen, M. and R. H. Wiley.

IV. HOMEOSTASIS OR STEADY STATE?

Quantitative description of the ontogenetic trajectories of individuals in a society immediately raises questions about the behavioral and physiological mechanisms that regulate these trajectories. To pursue our analogy with physics, we need to move from the kinematics to the dynamics of the movements of individuals through social positions.

At the outset of this review, we noted that one of the remarkable features of the relationship between individuals and societies is a relative constancy in the proportions or numbers of individuals in each social position in spite of the continual turnover of individuals. Such stable structure could arise either with or without feedback control of the recruitment of individuals to successive social positions. Feedback would consist of an inhibition of the recruitment of individuals to a particular social position as a function of the number of individuals already occupying that position. For instance, the presence of reproductive animals could inhibit the development of reproductive behavior in nonreproductive animals.

A stable social structure, however, need not require regulation by such feedback. If reproduction and mortality, along with the characteristics of individuals' ontogenetic trajectories, remained relatively constant over periods of many years, the social structure of such a population would reach a steady state. Any brief perturbations of the demography of such a population would result in corresponding alterations in social structure. The population would regain a steady social structure only over periods approximating the lifetimes of individuals and the durations of environmental perturbations. In contrast, feedback regulation of the succession of individuals to social positions would assure some homeostasis of the social structure in the face of demographic perturbations of the population.

In many social insects, the number of reproductives in a colony is under strong feedback control, mediated either by direct aggression of current reproductives against nonreproductives or by pheromones. Accumulating evidence also suggests that the ratio of soldiers to workers is under homeostatic control in some species (Wilson, 1971; Brian, 1979). No vertebrate society has received a comprehensive analysis of the mechanisms that regulate individuals' ontogenetic trajectories through social positions. Research on reproductive maturation in mammals, however, clearly establishes the possibility of feedback regulation of succession to reproductive social positions. In both male and female house mice, exposure to older reproductive individuals of the same sex inhibits reproductive maturation (Vandenbergh, 1974; Bronson, 1974). Exposure to reproductive individuals of the opposite sex, on the other hand, accelerates maturation. In house mice, both of these effects are stronger in females than in males. In fact, the inhibition of reproductive maturation by exposure to older males has a relatively slight, although reliable, effect on the maturation of younger males. In house mice these effects can result entirely from persistent olfactory stimuli in urine from reproductive animals.

Even if interactions with reproductive individuals fail to inhibit the maturation of younger individuals, resident animals might still prevent the establishment of young recruits in the population. This possibility has received a great deal of attention in discussions of territoriality in birds. At least in some species, established territorial residents exclude other individuals from optimal habitats. In some cases, like the great tit (*Parus major*) and the chaffinch (*Fringilla coelebs*), the excluded individuals find territories in less suitable habitats (Glass, 1960; Krebs, 1971). In red grouse, many excluded individuals fail to obtain territories at all. In this species, as we have noted, success or failure in obtaining a territory seems to have no relation to an individual's age. There is no ontogenetic progression from nonterritorial to territorial status or from suboptimal to optimal habitats. In other species though, young males are more common in suboptimal

habitats. In great tits, Krebs (1971) observed that males originally established in suboptimal habitats, hedgerows, moved their territories into optimal habitats, continuous woodland, when vacancies became available there.

Anecdotal information in the literature does not always allow a clear decision about the possibilities of feedback from social interactions in regulating the succession of individuals to reproductive status. The situation is particularly unclear for many polygynous species. In polygynous species, males begin to reproduce on average at a later age than do females. In many cases, they also reach full morphological and physiological development at a later age. For instance in polygynous birds like great-tailed grackles (*Quiscalus mexicanus*), red-winged blackbirds (*Agelaius phoeniceus*), and lek-forming species of grouse, males one year old have less developed plumage than older males, although they have already reached full weight. In addition the gonads of one-year-olds mature later in the breeding season than do older males' and never reach the full size of older males' (Wright and Wright, 1944; Selander and Hauser, 1965; Eng, 1963; Payne, 1969; Selander, 1972). In these species, one-year-old males rarely obtain territories suitable for reproduction.

On the basis of experiments in which older males have been removed from their territories and some young males have occupied their places, it is tempting to conclude that social interactions with older males inhibit reproductive development and behavior of young males. In fact, more careful examination of the evidence from removal experiments and some recent experiments with captive blackbirds suggest that, at least for grouse and blackbirds, social inhibition is unlikely to explain why young males fail to reproduce. In these blackbirds and in the lek-forming species of grouse, young males arrive on breeding grounds later in the season than do older males, in accordance with the later seasonal development of their gonads (Orians, 1961; Payne, 1969). In fact, for sage grouse, first-year males initially begin territorial behavior at the periphery of a lek about the time that copulations begin at the center, at least a month after the older males have started territorial activities. The territorial behavior of many first-year males barely overlaps with the period of copulation (Wiley, 1973).

In an experiment reported in the Russian literature (see Dementiev and Gladkov, 1967), Kirikov tried removing older males from leks of capercaillie (*Tetrao urogallus*) to see if younger males would establish territories earlier in the season. He reports that the presence of older males had no effect on the arrival dates of younger males, although in the absence of older males the younger males occupied the center of the lek. Thus although younger males occupied vacancies left on leks by older males, they only did so later in the season than older males normally began territorial activity.

Similar findings are reported for red-winged blackbirds. Again, although younger males will occupy vacancies left by the removal of older territorial males, they only do so late in the season after mating has begun for the females' first clutches (Orians, 1961). Earlier in the season, vacancies are reoccupied by other old males.

Thus the delay in maturation of the gonads and territorial behavior of first-year males is the critical factor in the regulation of their access to reproductive positions. In order to determine whether or not the seasonal course of physiological and behavioral maturation of first-year male red-winged blackbirds depends on direct social interactions with older males, Hartnett and I studied small groups of males in outdoor aviaries (Wiley and Hartnett, 1976). We compared three kinds of groups: three first-year males, one older male with two first-year males, and three older males. In each group one of the males became clearly dominant over the other two; in groups with mixed ages, the older male invariably became dominant. Thus we could compare the physiological and behavioral development of a dominant first-year male and dominant older males, all exposed to two subordinate first-year males. The dominant first-year males became as aggressive toward their subordinates as the older dominants did, but the increase in aggressive behavior proceeded more slowly during early spring than for the older males. As in the uncontrolled situation in the field, the dominant younger males became fully aggressive only in early May, about the time that most of the females lay their first clutches. Furthermore, the dominant young males had significantly smaller testes than the dominant older males in similar social situations. Dominance rank and exposure to older males thus had no major effects on the maturation of the gonads of first-year males. Contrary to our initial expectations, the behavioral and physiological development of young red-winged blackbirds seems largely independent of social interactions with older males.

So far we have focused on the mechanisms that regulate or generate the typical structure of a society. For this purpose we have concentrated on mechanisms that control the average parameters of the ontogenetic trajectories of individuals in the society. It is equally important to identify the factors that control the variation in ontogenetic trajectories. Although this variation would have little effect on the long-term or equilibrium structure of the society, it will have important effects in determining which of the available individuals eventually succeed to positions that permit successful reproduction.

For example, although most first-year male sage grouse establish territories around the peripheries of leks, there is substantial variation in the time during the season when they first become effectively territorial. Furthermore, among those males that survive to their second year, there is

undoubtedly substantial variation in the progress they make toward the center of the lek and successful reproduction. This sort of variation in ontogenetic trajectories depends on the relationships of individuals that occupy the same social position rather than, as before, the relationships of individuals occupying different social positions.

Fights between individuals provide one mechanism by which some individuals advance while others do not. Although direct aggression has undoubtedly importance as the court of last resort in deciding such matters, fighting is often nearly absent during the crucial movements of individuals into more advantageous positions. Sage grouse fight on their leks, occasionally severely, but these fights occur between established territorial males when one has transgressed its boundary. In contrast, when a vacancy occurs on a lek there is remarkably little fighting. In fact, the territory of a male that has suddenly disappeared often remains unoccupied for one or two days before a peripheral neighbor gradually begins to extend his activities into the vacancy. Even when two peripheral neighbors, to all appearances, have equal claims to the vacancy, there is no noticeable aggression. Similarly, in early spring when the first males begin to occupy positions on the lek, more than a month before the females arrive, agonistic interactions are infrequent and lackadaisical. At this time of year, toward the end of winter, leks are likely to have more vacancies than at any other time, and thus males should have the greatest opportunities for improving their positions.

Such observations suggest that differences in the advancement of individual males can depend more on their endurance and their luck than on direct aggression. Physiological endurance could have major effects here. Attendance at a lek in early spring requires some sacrifice in opportunities to feed. Those that can afford the necessary time at a lek might well stand to advance their positions. However, each male must balance these advantages against the possible disadvantages that would accrue from poor physiological condition as a result of insufficient time for feeding. Similar considerations might apply both to older males early in the spring, when snow is first disappearing, and to first-year males when they establish their territories for the first time toward the middle of the season. In general, similar considerations must apply to all individuals at the time they commence territorial behavior (Searcy, 1979b).

We cannot neglect the role of pure chance in determining variation in ontogenetic trajectories. For example, the leks of grouse are rarely exactly symmetrical around the central territories where most copulations occur. Thus the possibility arises that first-year males establishing territories at the periphery of a lek might find themselves at substantially different distances from the center. It would pay for a young grouse to make some assessment

of an optimal position to start its career on a lek, but in the absence of such an assessment the young male would have to take the luck of the draw. In addition, the opportunities for advancement presumably depend on the death of territory holders that intervene between a young male's initial position and the center of the lek. Thus the occurrence of vacancies for a young male to occupy is itself a random process that would introduce random variation in the ontogenetic trajectories of males.

Variations in the physiological condition of individuals and the chance availability of opportunities for advancement would generate considerable variation in the ontogenetic trajectories of individuals in any complex society. The importance of fighting in the advancement of individuals through successive social positions, on the other hand, might depend on whether or not orderly queuing can occur for reproductive positions.

Stripe-backed wrens are instructive in this regard, because fierce fighting is usual in advancement to reproductive status by females, but not males. When the reproductive male of a group disappears, one of the older males assumes the vacancy, usually with no signs of conflict within the group. On the other hand, when a reproductive female disappears, her vacancy becomes the subject of intense competition among females from nearby territories. Although invading females often come from as far as four territories away usually a female from a neighboring territory successfully claims the position. The first few days of the contest bring repeated, intense fighting between the presumptive females. Females peck each other viciously and grapple in midair. The auxiliary (nonreproductive) males in a group, like the males on a lek of grouse, participate in a queue for the principal (reproductive) position. Like the sage grouse, succession to reproductive status involves primarily an orderly progression of individuals into the available vacancies. The female stripe-backed wrens that compete for vacant reproductive positions in groups, in contrast, have not queued for this position. Although females from nearby territories have an advantage over those from farther away, the available females from different territories at roughly equivalent distances from a vacancy have had little opportunity for previous encounters. In the absence of opportunities for a slow contest of endurance, the females take the court of last resort and fight it out.

V. EVOLUTION OF MATURATIONAL CONTROLS

Our review of the mechanisms that could regulate individuals' ontogenetic trajectories leads to a question that is fundamental for understanding the evolution of social structure. We can no longer indiscriminate-

ly invoke "the good of the species or the group" in explaining the evolution of social behavior, the usual practice in previous generations. The first principle of any acceptable explanation for evolutionary adaptation is the accumulation in a population of those alleles, or combinations of alleles, that spread fastest and persist longest in a particular environment. How then can selection favor the evolution of maturational mechanisms that result in postponement of reproduction, the most direct effect of which is an increase in generation time?

Clearly the evolution of complex social structure in animals is inextricably associated with the evolution of an optimal allocation of effort to reproduction, growth, and maintenance throughout the life of an individual. In spite of the recent wave of interest among evolutionary biologists in the evolution of life-history strategies (Gadgil and Bossert, 1970; Stearns, 1976; Horn, 1978), very little of this approach has penetrated the study of animal societies. Even societies with contrasting structures, like those of stripe-backed wrens and sage grouse, present similar problems in the evolution of ontogenetic trajectories that represent optimal life-history strategies.

The reasons that students of animal societies have so far not fully acknowledged the literature on life-history strategies stem from the wide acceptance of at least three arguments inherited from long before modern advances in evolutionary theory. First is a tacit equation of behavioral competition (aggressive interactions) with evolutionary competition (relative rates of propagation of alleles in a population). Second is an assumption that older animals have an inevitable ability to exclude younger animals from opportunities to reproduce. Third are arguments that fixed behavior by one category of individuals, often one sex, unilaterally determines the evolution of another category of individuals.

First consider the problem of equating behavioral and evolutionary competition. Allee took this step when he inferred that dominant individuals had higher evolutionary fitness than subordinates. However, when we consider cases in which interacting individuals differ in age, the possibility arises that both act in accordance with optimal age-specific strategies, in spite of the fact that one dominates the other. In cases in which evolution favors increasing reproductive effort with age, older individuals should exert more effort in obtaining reproductive social positions than younger individuals. Nevertheless, at any age individuals should always avail themselves of opportunities to reproduce within the constraints of the optimal age-specific effort and risk. One can imagine situations in which individual adaptability in life-history strategy would prove evolutionarily adapted when environmental and demographic conditions changed markedly over periods of approximately an individual lifetime. At any rate, an uneven outcome of behavioral competition between individuals that differ

in age could well have no effect on the individuals' relative fitnesses. Uneven behavioral competition between individuals of the same age, on the other hand, would always influence their relative fitnesses.

The assumption that older animals have an inevitable advantage over younger animals in claiming opportunities for reproduction is well entrenched in the literature on the evolution of polygyny. Young males, it is argued, postpone full reproductive development and effort because they cannot compete with older males for mates and consequently have little chance of reproduction. It is true that in polygynous species younger males do not compete successfully with older males for mates. There are two possible explanations for this phenomenon. The traditional one goes as follows: young and old males inevitably differ in competitive abilities; consequently, when males have limited parental duties older males inevitably obtain most of the mates, the population becomes polygynous, and the males evolve delayed maturation. The other explanation runs as follows (Wiley, 1974a): when the fitness of males but not females is increased by delayed reproduction, males evolve deferred reproductive maturation and effort, provided that any consequences of reduced male parental care for breeding success do not counterbalance the advantages of sexual divergence in life histories; consequently, more females than males breed in a given season, which amounts to polygyny. Both explanations depend on ecological conditions that reduce the advantages of full parental care by males (Verner, 1964; Orians, 1969). The first explanation requires an assumption that males cannot evolve full competitive abilities at an early age under any circumstances. The argument hinges on an inevitability of increased competitiveness with age. It thus assumes the consequent. If this assumption of inevitability were not accepted, one would have to explain the evolution of increased competitiveness with age or, the other way around, decreased competitiveness at early ages. In effect, the inevitability assumption is the primary distinction between the two explanations for the evolution of polygyny. In addition to this theoretical objection to the inevitability assumption, the red grouse provides a counter example. In this species, first-year males and older males compete equally for territories. The second explanation above emphasizes two factors in the evolution of polygyny: the adaptedness of life-history strategies of males and the adaptedness of parental strategies.

The two-factor theory of the evolution of polygyny has some similarities to Maynard Smith's (1977, 1978) analysis of parental care. In explaining the evolution of heterosexual relationships, both approaches consider the consequences of the male's strategy as well as the pattern of parental care. Maynard Smith's analysis in terms of game theory focuses on the relative survival of eggs under the care of two, one, or no parents; the tradeoff for a female between producing eggs and guarding them after lay-

ing; and the possibilities of additional matings for males that desert their first partners. Maynard Smith considers two strategies for each sex, either caring for the young or deserting. He then establishes the conditions that make each of the four possible patterns of parental care advantageous for each sex, an analysis that elegantly clarifies the interacting influences on the evolution of parental care and mating systems.

This approach converges closely with the two-factor theory for the evolution of polygyny when we consider that the possibilities for additional matings by deserting males are associated with sexual bimaturism, a delay in the age of reproduction by males relative to females. As indicated above, increased fecundity of males in polygynous species is, in large part, associated with delayed reproduction. Thus the analysis must consider the effects of age-specific fecundity and survival on the fitnesses of a male's genes. In the end, a full analysis of the evolution of mating systems will require assessment of the balance between the adaptedness of sexual bimaturism and the adaptedness of different patterns of parental care.

The third problem that impedes applications of life-history theory to social behavior has, like the second, appeared particularly in explanations for the evolution of polygyny. It has often been proposed that females prefer to mate with older males or with males that have already attracted other mates, because such males have demonstrated exceptional abilities to survive or reproduce. The fundamental approach here is sound: females should evolve behavior that results in mating with males that have the highest fitness. However, modern theory of life-history strategies teaches clearly that fitness is not a simple function of survival to old age nor of fecundity in any one season. Females should indeed evolve behavior that results in choosing mates with the highest fitness, but a male's fitness depends on his age-specific allocations of effort to survival and reproduction throughout his life. In this view, the evolution of female preferences converges with the evolution of optimal male life-history strategies. An explanation for the adaptedness of delayed reproduction and high fecundity at a late age among males is basic to understanding the evolution of female preferences in polygynous species.

A deferment of reproductive effort is often not absolute. In polygynous species, for instance, males often initiate a low level of reproductive effort a year or more before they have any real opportunity for success. In fact, these young males sometimes channel their reproductive effort in ways that offer little chance of success even if an opportunity should arise unexpectedly. First-year male sage grouse and red-winged blackbirds, for instance, only mature to full agonistic behavior after the main period of mating has begun. Why do they bother to take any risks of territorial behavior their first year at all?

The answer here could well relate to the queuing effect. It might pay for a first-year male to establish his territorial position, particularly late in the season after the most intense territorial competition has passed, in anticipation of improving his chances for a good territorial position and mating success the next year. On grouse leks, territorial vacancies are usually occupied by established neighbors and almost never by newcomers that arrive abruptly from outside. A male sage grouse probably gets to the head of the line by alertly occupying vacancies as they arise ahead of him. As for red-winged blackbirds, recent evidence suggests that a male's success in attracting females relates in part to having occupied its territory in the preceding year (Searcy, 1979a; Yasukawa, 1979). Exactly why previous occupation of a territory confers an advantage in attracting females is not clear. Possibly males with previously established territories can reoccupy them on average earlier in the season, and perhaps with less agonistic behavior as well, and these two consequences in turn result in greater success in attracting females. At any rate, in these two dissimilar polygynous species young males seem to establish territories late in their first year primarily in anticipation of benefits that accrue for successful mating in subsequent years.

In societies with cooperative breeding, like the stripe-backed wren, most members of a group are usually genealogically related. As a consequence, kin selection influences the evolution of interactions between group members (Brown, 1978; Emlen, 1978). Most of the information available so far about the genealogical relatedness of group members consists of reports that young join their natal group as auxiliary members. Auxiliaries early in life are thus likely to be the progeny of the group's principal members. Few studies, however, have documented the steps by which individuals become principal members of groups. In stripe-backed wrens, a new female principal is normally a newcomer from outside the group and thus usually has low genealogical relatedness to the group's current auxiliaries. A new male principal, on the other hand, is often a sibling or half-sibling of the auxiliaries in the group. Consequently, as an auxiliary member of a group grows older and one or both principals change, its genealogical relatedness to the principals usually decreases. The behavior of an auxiliary, as a result of kin selection, should depend on whether or not the principals have changed since it joined the group at birth. The expected genealogical relatedness of the principals to an auxiliary of any age results directly from the ontogenetic trajectories of individuals in the population.

The evolution of ontogenetic trajectories in societies with cooperative breeding also requires examination in relation to deferred reproduction. The delay in reproduction by the auxiliary members of groups raises the same problems as the delay in reproduction by males in polygynous societies. A full explanation for the evolution of societies with cooperative breeding will

thus require consideration of the genealogical relationships of group members, the consequences of participation in groups for the immediate survival and reproduction of individuals in each social position, and the consequences of delayed reproduction (Brown, 1978; Emlen, 1978; Gaston, 1978; Wiley, 1978; Rabenold and Christensen, 1979).

The evolution of deferred reproduction, a critical concern in the preceding discussion, depends on an interaction of several aspects of age-specific survival and reproduction. Evolution of reproduction starting at a given age a will depend on the chances of survival to age a , the expected fecundity at age a , the rate of increase of the population, and the consequences of reproduction at age a for the chances of survival to the next breeding season and for future fecundity.

To see these interacting influences on the evolution of delayed reproductive effort, we can use the standard equation for the rate of population increase,

$$1 = \sum_a \lambda^{-x} l(x) m(x)$$

where λ is the proportionate annual population increase (N at $t + 1/N$ at t), $l(x)$ is age-specific survival, $m(x)$ is age-specific fecundity, and a is the age at first reproduction. This equation applies to any lineage of organisms, provided age-specific survival and fecundity remain constant with time and the lineage has had time to reach a stable age-distribution. For diploid organisms, λ provides only an approximate measure of the fitness of an allele associated with a set of age-specific parameters (Charlesworth, 1973). As a first step though, we can ask whether lineages with particular age-specific parameters increase more rapidly than lineages with other parameters. This approach rests on the basic tenet of evolutionary biology: those alleles that propagate fastest accumulate in a population.

Consider two lineages: in one, individuals begin to reproduce at age a ; in the other, individuals begin to reproduce at age $a + 1$ and, as a consequence, have higher survival by a factor S between ages a and $a + 1$ and also have higher fecundity by a factor M at age $a + 1$ and thereafter. Thus:

$$l_2(x) = S l_1(x), \quad x \geq a + 1, \quad S \geq 1 \quad (1)$$

$$m_2(x) = M m_1(x), \quad x \geq a + 1, \quad M \geq 1 \quad (2)$$

To proceed with our derivation, write the equations for λ for the two strategies as follows, by separating the terms for age a and substituting from equations (1) and (2):

$$1 = \lambda_1^{-a} l_1(a) m_1(a) + \sum_{a+1}^{\infty} \lambda_1^{-x} l_1(x) m_1(x) \tag{3}$$

$$1 = SM \sum_{a+1}^{\infty} \lambda_2^{-x} l_1(x) m_1(x) \tag{4}$$

Subscripts indicate strategies 1 and 2. Note that under these assumptions reproduction at age a has no effect on annual mortality in any year other than between a and $a + 1$, while reproduction at age a can affect annual fecundity at all later ages. We consider below conditions under which delayed reproductive effort might increase survival ($S > 1$) during the year in which reproduction is deferred or increase fecundity ($M > 1$) in later years.

If we now ask for the conditions under which $\lambda_2 = \lambda_1$, the summations in equations (3) and (4) become equal. Substituting from equation (4) into equation (3), we have

$$\frac{SM - 1}{SM} = \lambda^{-a} l_1(a) m_1(a), \quad \lambda_2 = \lambda_1 = \lambda$$

For the conditions under which λ_2 is greater than, or less than, λ_1

$$\frac{SM - 1}{SM} \begin{matrix} \gg \\ \ll \end{matrix} \lambda_1^{-a} l_1(a) m_1(a), \quad \lambda_2 \begin{matrix} \gg \\ \ll \end{matrix} \lambda_1$$

If strategy 1 yields a stable population, so that $\lambda_1 = 1$, then

$$\frac{SM - 1}{SM} \begin{matrix} \gg \\ \ll \end{matrix} l_1(a) m_1(a), \quad \lambda_2 \begin{matrix} \gg \\ \ll \end{matrix} \lambda_1 = 1 \tag{5}$$

This equation relates the probability that an individual can replace itself in the population by reproducing at age a , $l(a)m(a)$, and the consequences of reproduction at age a on its future chances for reproduction, SM . When $\lambda_2 > \lambda_1$ for animals in a particular environment, a lineage of individuals that delay reproduction to age $a + 1$ will multiply faster than a lineage of individuals that begin reproduction at age a (see Appendix and Wittenberger, 1979).

All four parameters in equation (5) can be measured in natural populations; $l(a)$ and $m(a)$ are respectively survival to age a and fecundity at age a if an individual tries to breed. Determinations of S and M depend entirely on comparing two separate sets of individuals in a population, those beginning to breed at some age a and those that defer reproductive attempts until one year later. S is the proportionate change in survival of individuals that defer reproduction, the survival between ages a and $a + 1$ of individuals deferring reproduction divided by the survival of individuals with early reproduction. M

is the proportionate change in the eventual fecundity of individuals that defer reproduction, the fecundity at any age $\geq (a + 1)$ of individuals that begin reproducing at age $a + 1$ divided by that of individuals that begin reproducing at age a . Note that M is *not* the ratio of fecundity at age a to that at age $a + 1$; it is the ratio of fecundities of individuals with different life-history strategies but with the same age $\geq (a + 1)$. A number of studies of natural populations of animals have shown that individuals have lower fecundity in their first year of reproduction than at later ages. I know of none, however, that compares individuals of the same age after they had begun reproduction at different ages. Wooller and Coulson (1977) have made a start in this direction.

In an earlier publication, I derived in a similar way a slightly different expression for the conditions under which delayed reproduction would evolve (Wiley, 1974b). That derivation involved different assumptions about the differences between an early reproducing and a late reproducing strategy and resulted in a somewhat different set of conditions for the evolution of deferred breeding. In particular, my earlier derivation assumed that deferred reproduction resulted in a translation of the function for age-specific fecundity $m(x)$ to later ages, so that $m_2(x + 1) = Mm_1(x)$, where subscripts 1 and 2 indicate strategies that begin reproductive effort at ages a and $a + 1$, respectively. Under this assumption, if individuals beginning to reproduce at age a have lower fecundity in their first year than later in life, then individuals deferring reproduction would also have lower fecundity in their first year of breeding than later. The fecundity of a first-time breeder at age $a + 1$ might still be larger by a factor M than the fecundity of a first-time breeder at age a . Under these conditions, deferred reproductive effort in a stable population should evolve when

$$AM > 1$$

where A ("As" in the terminology of Wiley, 1974b) equals the survival between ages a and $a + 1$ of individuals that begin reproduction at age a . In both of these formulations, when individuals that defer reproduction have high survival between ages a and $a + 1$ and high fecundity at ages $\geq (a + 1)$, then lineages of individuals with these characteristics tend to spread at the expense of those in which individuals begin reproduction earlier.

Deferment of reproductive effort could plausibly increase an individual's survival. The time and energy spent in reproductive activities, such as maintenance of a territory and advertisement activities, could instead be devoted to feeding and hiding from predators. There are very few data available, however, to test this possibility directly. Recent information suggests that male sage grouse survive better between ages 1 and 2 than when older (Beck and Braun, 1978). A direct test of the theory, however, would require a

comparison of the survival of males in relation to their reproductive effort at age 1.

Deferred reproductive effort might increase later fecundity in several ways. A clear case is provided by animals with indeterminant growth. Early reproduction entails a diversion of resources from growth with the consequence that the animal is smaller in size at all subsequent ages, and size in animals with indeterminant growth usually correlates with fecundity. In addition, social organization that provides the possibility of queuing for advantageous reproductive positions also raises the possibility that at least partial deferment of reproductive activity could result in increased fecundity at later ages.

To test the theory we need comparisons of individuals that begin reproductive effort at early ages, without taking their places in queues of social positions, and individuals that at least partially defer reproductive effort by participating in queues. Certainly the magnitude of a male's eventual fecundity is substantial in lek-forming species like the sage grouse (see Wiley, 1974a). In addition, in at least some birds that live in stable social groups with one reproductive pair, groups are substantially more successful in reproduction than individuals that breed as pairs without nonreproductive helpers (Rowley, 1965; Woolfenden, 1975; Brown, 1978; Rabenold, personal communication). In both cases, we lack sufficient information for a thorough evaluation of the evolution of deferred reproduction. The key data will come from comparisons of the life-history parameters of individuals that pursue different strategies of reproductive effort early in life.

In analyzing the evolution of deferred reproduction, we have focused on the optimal age for an individual to begin reproduction on the basis of the rate of propagation of genes influencing the onset of reproductive activity. Although equation (5) compares the advantages of starting reproduction at only two ages, a and $a + 1$, it can also serve to determine the optimal age for starting reproduction. Just compare successive ages in pairs until at some age the conditions for further delay in the onset of reproduction no longer obtain. This optimal age for the onset of breeding will depend on the age-specific values of l_a , m_a , S , and M , the expected survival and fecundity at any age a , and the consequences of reproduction at age a on future survival and fecundity.

This analysis has not considered the possibility that alternate strategies for reproductive maturation might coexist stably in the same population. Some individuals might begin reproduction at an early age by parasitizing older individuals at the head of a queue, for instance by clandestinely stealing copulations or laying eggs in the nests of older animals. These individuals would thus jump the queue. In stripe-backed wrens, for instance, occasional (<5%) female auxiliaries develop full brood patches and thus could possibly have produced

eggs. An occasional male auxiliary develops an unusually close association with the principal female of its group and might possibly copulate with her. In a diversity of species in which males defend locations at which they copulate with females, some males do not display and clandestinely steal copulations with females inside the areas defended by displaying males (Hogan-Warburg, 1966; van Rhijn, 1973; LeBoeuf, 1974; Constantz, 1975; Wells, 1977; Perrill *et al.*, 1978; Howard, 1978).

Alternate strategies in the same population might constitute an evolutionarily stable mixed strategy (mixed ESS; Maynard Smith, 1974, 1976). When the successes of individuals using each strategy depend on their relative frequencies in the population, equilibrium frequencies could exist that would result in equal success for both strategies. Either individuals could change from one strategy to the other, with the proportions of time spent using each corresponding to the equilibrium frequencies, or individuals could each use one strategy, with the proportions of the different kinds of individuals in the population corresponding to the equilibrium frequencies. If the ages of individuals using the two strategies had different distributions, an analysis of the fitnesses of genes influencing the two strategies would have to consider fecundity and survival as functions of age for individuals with each strategy.

When individuals change their behavior progressively with age, the behavioral differences among individuals in a population might instead represent age-specific manifestations of a single optimal life history. In particular, when younger individuals can occasionally parasitize the reproductive success of older individuals without much effort or risk, they should do so, even when an optimal life history involves a deferment of more intense reproductive activity to later ages. If risk and effort are low, then the consequences of opportunistic reproduction for future survival and fecundity are likely to be small, and $(SM - 1)/SM$ in equation (5) will approach 0. Individuals should never pass up opportunities for reproduction that costs very little. When young individuals at the tail of a queue occasionally parasitize the reproductive advantages of older individuals at the head of a queue, the possibility thus exists that each individual pursues an optimal age-specific strategy.

VI. CONCLUSION

This article began with a suggestion for describing the movements of individuals through social positions in terms of ontogenetic trajectories. This approach led to several fundamental questions about the regulation of the ontogenetic trajectories of individuals in a society. Even the very little that we can now conclude about the mechanisms controlling ontogenetic trajec-

tories led in turn to some fundamental evolutionary questions. Although the recent interest in animal societies has concentrated on the evolution of social behavior, nevertheless our perspective on ontogenetic trajectories as a basic feature of societies has uncovered some neglected evolutionary questions. A more thorough investigation of ontogenetic trajectories in animal societies, the behavioral and physiological mechanisms that control them, and their evolutionary adaptedness promises to open some new chapters in our understanding of societies as interacting individuals.

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VIII. APPENDIX

Wittenberger (1979) has also obtained an expression for the conditions that favor the evolution of deferred reproduction. His formula is identical to my equation (5) with $M = 1$, although some algebra is necessary to see this identity. His condition for the evolution of deferred reproduction in a stable population is

$$\frac{b(\alpha - 1)}{b(\alpha)} < \frac{\Delta s}{1 - s(\alpha)} \quad (\text{A-1})$$

where $b(\alpha - 1)$ is the fecundity of an individual breeding at age $x = \alpha - 1$, $b(\alpha)$ is the fecundity of all individuals at ages $x \geq \alpha$ regardless of earlier breeding, $s(\alpha)$ is the annual mortality of individuals at ages $x \geq \alpha$, and

$$\Delta s = s(\alpha - 1) - s'(\alpha - 1)$$

the difference in annual survival between individuals that breed at age $x = \alpha - 1$ (with prime) and individuals that defer reproduction to age

$x = \alpha$. Rearranging this expression, we obtain

$$b(\alpha - 1) < \Delta s \cdot b(\alpha) \sum_0^{\infty} s(\alpha)^z$$

where $z = x - \alpha$. Note that in a stable population

$$b(\alpha)l(\alpha) \sum_0^{\infty} s(\alpha)^z = 1$$

where $l(\alpha)$ is the survival from age 0 to age α .

Consequently Wittenberger's formula reduces to

$$b(\alpha - 1) < \Delta s / l(\alpha) \tag{A-2}$$

Now consider my equation (5) with $M = 1$. My S equals, in Wittenberger's terminology, $s(\alpha-1)/s'(\alpha-1)$, and my $l(\alpha)$ equals $l(\alpha)/s(\alpha-1)$. Thus (5) with $M = 1$ reduces to (A-2) above.

Equations (A-1) and (A-2) and equation (5) with $M = 1$ are equivalent conditions for the evolution of deferred reproduction in a stable population, when early reproduction has no effect on an individual's later fecundity. Wittenberger's application of equation (5) to males of polygynous species follows the traditional explanation for the evolution of polygyny in contrast to my two-factor theory.

Although Wittenberger (1979, p. 439) states that my earlier derivation (Wiley, 1974b) assumes constant fecundity throughout life for each strategy, in fact $m(x)$ in my derivations can take any form whatever. In addition, my derivations by incorporating the factor M include the possibility that early reproduction can influence later fecundity.

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