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PITVIPER MATING SYSTEMS: ECOLOGICAL POTENTIAL, SEXUAL SELECTION, AND MICROEVOLUTION

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ABSTRACT: Free-ranging pitvipers and other snakes represent potentially good subjects for predictive analyses of pattern and variation in male-male competition, sexual selection, relationships between mating success and fitness, polygyny, and mating system structure. Pitviper systems also facilitate simultaneous considerations of the effects of ecological potential and proximate constraints on mating system structure and variation. We discuss some relevant models and predictions, as well as empirical data collected on a population of free-ranging radiotagged pitvipers, that substantiate some of our propositions and that suggest directions for future work.

INTRODUCTION

Animals vary locally, geographically, and taxonomically in mating strategy, reproductive success, and social structure. For example, males of some taxa defend access of other males to females and even the habitats the latter may occur in, others scramble in competitive searches for females, and yet others exhibit no competition whatsoever for access to mates (Darwin, 1871; Wells, 1977; Alcock, 1980; Halliday, 1980; Wittenberger, 1981; Thornhill and Alcock, 1983; Gwynne, 1991). Likewise, males and females in different taxa vary in relative simultaneous numbers of matings and associated levels of reproductive success or fitness (e.g., Bateman, 1948; Wade and Arnold, 1980; Clutton-Brock, 1988). It also appears that local ecological circumstances (Emlen, 1976; Emlen and Oring, 1977; Sullivan, 1989; Ims, 1990) and proximate constraints (= phylogenetic, morphological, physiological, and so forth; Halliday, 1987; c.f., Whittier et al., 1985; Crews and Moore, 1986; Whittier and Crews, 1990) exert effects on pattern and variation in reproductive strategy. Considered broadly, these many approaches and observations may be said to comprise the analysis of mating systems. Of particular relevance to this chapter are the observed and expected mating systems of snakes in general and the pitvipers in particular.

Analyses of animal mating systems have increased in number and generality in recent years (e.g., Wells, 1977; Bateson, 1983; Thornhill and Alcock, 1983; Vehrencamp and Bradbury, 1984; Bradbury and Andersson, 1987; Sullivan, 1989; Schwagmeyer, 1990). This situation has been affected by (a) the development and refinement of predictive theory (Orians, 1969; Parker, 1970, 1978, 1984; Emlen and Oring, 1977; Trivers, 1972; Thornhill, 1986; Hammerstein and Parker, 1987; Gwynne, 1991; c.f., Maynard Smith, 1987), (b) a natural interface between work on mating systems and sexual selection (Darwin, 1871; Bateman, 1948; Howard, 1979; Payne, 1979; Wade, 1979, 1987; Wade and Arnold, 1980; Arnold, 1983, 1985, 1986; Halliday, 1983; Thornhill and Alcock, 1983; Sutherland, 1985 a, b, 1987; Kirkpatrick, 1987; Verrell, 1989), (c) the realization of the importance of local ecological potential for certain reproductive strategies and not others (e.g., Orians, 1969; Emlen and Oring, 1977; Alcock, 1980; Vehrencamp and Bradbury, 1984; Ims, 1988, 1990), (d) the recognized importance of proximate constraints (Halliday, 1987), and (e) the tractability of empirical work, even in the field (e.g., Payne and Payne, 1977; Kluge, 1981; Thornhill and Alcock, 1983; Woodward, 1984; Sullivan, 1989).

Much remains to be done, however. Predictive theory and models remain largely conceptual rather than quantitative in nature (but see, for example, Parker, 1970; Kluge, 1981; Wade and Arnold, 1980; Arnold and Wade, 1984 a, b; Sutherland, 1985 a, b, 1987; Ims, 1988; Arnold and Duvall, under review). This has led to some confusion or at least differences of opinion about definitions and, thus, appropriate problems for study (Kluge, 1981; Sutherland, 1987; Grafen, 1987, 1988). Generally, animal mating systems have been defined in terms of variance in the relative simultaneous numbers of successful matings by males and females during meaningful reproductive time periods (e.g., Emlen and Oring, 1977; Halliday, 1980; Thornhill and Alcock, 1983; Shields, 1987). The latter may be seasons or, ideally, lifespans (e.g., Howard, 1983; Clutton-Brock, 1988).

Snakes in general, and the pitvipers (subfamily Crotalinae; e.g., Smith and Brodie, 1982) in particular, have not been popular for predictive behavioral studies in nature. However, we hope to demonstrate that they are good subjects for studies of social structure as reflected in mating systems (c.f., Prater, 1933; Brattstrom, 1974; Gillingham, 1987). They are especially suitable for theory and predictions relevant to cases where (a) male competition and associated potential intrasexual selection may explain taxonomic and geographical variation in mating systems and social structure (Duvall, under review; see below), and (b) female choice, parental care, and nuptial gifts presented by males to females, play little or no role in the accrual of individual fitness or reproductive success. Additionally, active mate choice by female snakes has not yet been observed in nature. Having noted these many points, however, we are aware that little information exists of the sort necessary to formally and quantitatively analyze snake mating systems (but see Shine, 1978; Shine et al., 1981; Gillingham, 1987; Slip and Shine, 1988; Graves and Duvall, 1990; King and Duvall, 1990). Accordingly, we summarize below some of our own findings that seem relevant, in order to provide empirical context for theoretical propositions developed here and to suggest some directions for further work. We also present a predictive classification of pitviper mating systems.

Most importantly, however, we summarize quantitative

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predictions relevant to pitvipers and other snakes, as derived from a more complete set of microevolutionary models of sexual selection and associated animal mating systems developed by Arnold and Duvall (under review). These formulations are based in part upon encounter rate models (e.g., Holling, 1959; Parker, 1970; Baylis, 1981; Sutherland, 1985 a, b), some of these in turn derived from renewal theory (Cox, 1962), and selection theory (Crow, 1958; 1986; Lande, 1979; Wade, 1979, 1987; Wade and Arnold, 1980; Arnold, 1983, 1985, 1986; Lande and Arnold, 1983; Arnold and Wade, 1984 a, b; Trail, 1985; Endler, 1986; Kirkpatrick, 1987). Thus, predictions derived should be of use to empirical biologists interested in the microevolution of suites of behavioral, physiological, and/or morphological traits associated with sexual performance in the context of mating systems and sexual selection. We also discuss a few relevant predictions from the computer simulation model RattleSnake© (Duvall et al., 1989, under review; Mintzer et al., 1992), which can formalize expectations about efficacious geometry for two dimensional search paths, given different spatial distributions of resources (e.g., potential mates and/or resources important to them). Efficient searching for mates is a critical component both of our theoretical formulations and many snake mating systems.

AN INTRODUCTION TO PITVIPER MATING SYSTEMS

All evidence to date suggests that most snakes, including the pitvipers, are polygynous. Therefore, we expect males to exhibit greater variation than females in numbers of matings (= mating success) per reproductive period. Another way to say this is that males exhibit a greater, relative simultaneous number of matings per reproductive period than do females. This expectation has several sources. First, potential energetic costs per unit offspring are much greater in female snakes than in males. Second, potential lifetime reproductive output is greater for males than for females. And third, covariance between mating success and fitness (or the sexual selection gradient; see below) is stronger and more positive among males than in females. Thus, we hypothesize that parental investment per unit offspring is relatively high among females, and that they are a scarce resource over which males should compete (Bateman, 1948; Trivers, 1972; Gibson and Falls, 1975; Alcock, 1980; Parker, 1984; Sutherland, 1985 a, b; Thornhill, 1986; Gwynne, 1991; Arnold and Duvall, under review). Accordingly, the potential for polygyny among the snakes is high.

To expand briefly, costs of vitellogenesis and folliculogenesis per potential offspring for female pitvipers, whether viviparous or oviparous, are extreme relative to those experienced by males in spermatogenesis. The maximally effective reproductive strategy for most female snakes, therefore, will be to forage, feed, and thermoregulate as effectively as possible (e.g., Charland and Gregory, 1989; Huey et al., 1989; Duvall and Chiszar, 1990; Duvall et al., 1990b). Female prairie rattlesnakes *(Crotalus viridis viridis)* exhibit broad swings in body mass during their typically lengthy reproductive cycles, or when pregnant versus post partum, due to the extreme costs of vitellogenesis per unit offspring. Males, conversely, generally exhibit energetically less expensive, small and regular increments in body mass as they grow (Graves and Duvall, 1990, under review; Duvall et al., unpublished data; c.f., Parker and Plummer, 1987). Indeed, females of several taxa, especially temperate forms (Rahn, 1942; Glissmeyer, 1951; Fitch, 1970; Aldridge, 1979 a; Bull and Shine, 1979; Diller and Wallace, 1984; Gannon and Secoy, 1984; Macartney and Gregory, 1988; Charland and Gregory, 1989; Graves and Duvall, under review), require more than one and sometimes even three seasons of feeding and vitellogenesis to produce a single clutch or litter (Klauber, 1936; Tinkle, 1962; Wharton, 1966; Shine, 1981; Gibbons, 1972; Bull and Shine, 1979; Blem, 1981, 1982; Fitch, 1982; Solórzano and Cerdas, 1989; but c.f., Wallace and Diller, 1990). Males, conversely, typically exhibit annual spermatogenic cycles even in temperate regions (Rahn, 1942; Ludwig and Rahn, 1943; Aldridge, 1979 b; Duvall et al., 1982; Saint Girons, 1982), and thus are potentially able to mate each season. Male snakes produce large quantities of sperm relative to numbers of primary follicles in female snakes (Mengden et al., 1980); thus on theoretical grounds males have the potential to sire many offspring (Parker, 1984).

The existence of male-biased operational sex ratios (OSRs; Table 1) is another factor that may generate male-male competition, potential sexual selection forces, and polygynous mating systems in many pitviper populations (Emlen, 1976; Emlen and Oring, 1977; King and Duvall, 1990; c.f., Schuett and Gillingham, 1989). We define the OSR here as the ratio of potentially breeding males to females in a population. Male-biased sex differences in the numbers of reproductively receptive pitvipers appear to arise for a number of reasons. First, absolute population sex ratios are unity or close to it (e.g., Klauber, 1936; King and Duvall, 1990; Duvall, under review). Second, females of many forms appear to be sexually receptive in only one or two seasons of a lengthy (i.e., up to four seasons or years; Graves and Duvall, 1990, under review) and energetically expensive reproductive cycle, as described above (e.g., Graves and Duvall, under review). Intermittent sexual receptivity among prairie rattlesnakes appears to be the case because females probably are sexually nonreceptive in early stages of folliculogenesis (i.e., when immediately post-partum) and definitely are nonreceptive during the entire season in which they are gravid or pregnant (King and Duvall, 1990; Graves and Duvall, under review; Duvall, under review). Body size (Blem, 1981, 1982; Graves and Duvall, 1990, under review) and seasonal abundance of warmth and food in populations (Klauber, 1972; Diller and Wallace, 1984; Macartney and Gregory, 1988; Charland and Gregory, 1989; Wallace and Diller, 1990) likely affect the rate of female pitviper reproduction and, perhaps, local pattern and variation in OSR (Figure 1; c.f., Klauber, 1936; Fitch, 1970). Thus, both (a) iteroparity and the rate of female pitviper reproduction in populations and (b) variable seasonal windows of female sexual receptivity, combine to generate proximate constraints (e.g., Halliday, 1987) on male strategy and mating system structure in the pitvipers. Gibbons (1972), Tinkle (1962), and Wharton (1966), however, have suggested that female reproductive cycles of two or more years in duration may occur in some southern populations of pitvipers, suggesting that the relationships hypothesized in Figure 1 may be somewhat oversimplified.

It should be noted, however, that OSRs are difficult to measure accurately in nature (Kluge, 1981; but see Sullivan, 1989), and other statistics such as the breeding sex ratio (BSR; see below; Table 1), or the ratio of actual numbers of male and female *parents* in a population, may be more useful and predictive (Arnold and Duvall, under review). This is because the BSR reflects more precisely relative population sexual selection forces acting on males and females. Additionally, the form and extent of OSR-related, sexual selection effects may vary widely and unpredictably, and depend on local biotic and abiotic variables (e.g., Ims, 1988).

When male-male competition occurs, snake mating systems may take different forms and may be associated with very different selection pressures, depending upon local ecological potential. In parts of Wyoming, for example, where receptive females are few, spatially unpredictable, and far removed from the den, male-male fighting appears to be the exception and competitive mate searching the rule (Duvall, under review; King and Duvall, 1990; c.f., Schwagmeyer and Woontner, 1985, 1986). Males in some of these populations rarely encounter conspecific males or females when away from the den. Thus, little sexual selection is expected to operate on traits associated with fighting, since males rarely encounter same-sex conspecifics. Conversely, male copperheads (*Agkistrodon contortrix;* Fitch, 1960; G. W. Schuett, unpublished data) and a viperine snake, *Vipera berus* (Viitanen, 1967; Prestt, 1971; Andrén, 1986; Saint Girons et al., 1989), for example, occur regularly in close proximity to other males and receptive females (c.f., Lowe et al., 1986). Accordingly, males of these and certain other pitviper and viper taxa have been observed to fight (Shine, 1978; Gillingham, 1987; Schuett and Gillingham, 1989). Among temperate garter snakes *(Thamnophis)*, for example, in which sexually receptive males and females are clustered tightly in time and space upon emergence in spring from hibernation at the den or hibernaculum opening, explosive mating assemblages ensue (e.g., Gardner, 1955; Gregory, 1974; Joy and Crews, 1988; Graves and Duvall, 1990; c.f., Garstka and Crews, 1982). These assemblages truly comprise "scrambles" by the many males for the few females, as the latter emerge over periods ranging from a few to several days. Similar mating systems may arise where male pitvipers experience similar female spatial and temporal distribution sets.

Table 1. Variables comprising mating system and related models.

Variable	Definition
$\bar{m}_f$	Average fitness (= fecundity or progeny count) of females that mate once or more.
$\bar{m}_m$	Average fitness of males.
$\bar{X}_f$	Average female mating success (= number of mates).
$\bar{X}_m$	Average male mating success.
H_x	Harmonic mean mating success of females with one or more mates.
$\sigma^2_{x \cdot f}$	Variance in mating success for all females (including the zero class with no mates).
$\sigma^2_{x \cdot m}$	Variance in mating success for all males.
q	Female mating failure (proportion of females capable of breeding that do not).
$\beta_{ss \cdot f}$	Female sexual selection gradient.
$\beta_{ss \cdot m}$	Male sexual selection gradient.
OSR	Operational sex ratio (the average over time of the number of sexually active males to the number of females capable of insemination).
BSR	Breeding sex ratio (= parental ratio; ratio of number of breeding males to number of breeding females).
L	Length of mating season.
s	Mate searching time.
h	Mate handling time.
c	Mate cycling time (= s + h).
p	Mate persuasion efficacy.
α_s	Average mate searching time.
α_h	Average mate handling time.
α	Average mate cycling time (= $\alpha_s + \alpha_h$).
α_p	Average mate persuasion efficacy.
$\beta ss\text{-}\alpha_s$	Sexual selection gradient for average searching rate.
$\beta ss\text{-}\alpha_h$	Sexual selection gradient for average handling rate.
$\beta ss\text{-}\alpha$	Sexual selection gradient for average mate cycling.
$\beta ss\text{-}\alpha_p$	Sexual selection gradient for average mate persuasion.
σ^2	Variance in mate cycling time.
σ^2_p	Variance in mate persuasion efficacy.
I_s	Potential for sexual selection (variance in mating success standardized to a mean of 1; = $s^2/\bar{x}^2$).

Yet another reason to expect polygyny among pitvipers is that mate monopolization potential by males is low. First, females appear to become sexually nonreceptive, or at least unattractive, to males after copulation, for periods that may range from several days, to weeks, or even the remaining duration of an active season (Devine, 1977; Ross and Crews, 1977; Whittier et al., 1985; Whittier and Crews, 1986; Schuett and Gillingham, 1988; Schuett, this volume; Duvall, under review). Females nevertheless may mate more than once per season prior to ovulation of a single clutch or litter. Thus, long-term mate monopolization by males is unlikely.

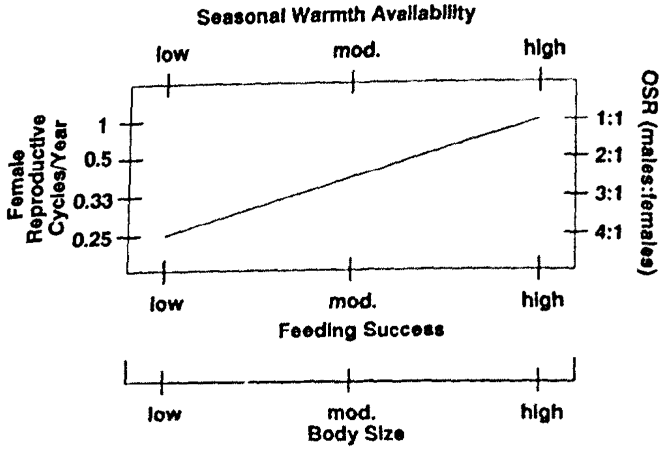

Fig. 1. Ecological and proximate variables hypothesized to be associated with the yearly rate of female prairie rattlesnake reproductive cyclicity and, in turn, local operational sex ratios (OSRs). The OSR is defined as the ratio of sexually active males to females in a population. We assume that population absolute sex ratios are unity. The hypothesized regression function derives from the literature and some of our own work. See text for discussion.

The presumed benefits of true mate-guarding monogamy (Thornhill and Alcock, 1983) are, therefore, expected to be minimal in the majority of pitvipers.

In order for a male to successfully monopolize an individual female over the entire duration of the receptive period or through her full reproductive cycle, he would have to guard her for one and, perhaps, even two full seasons, and this seems unlikely given other aspects of pitviper biology. Because large numbers of snakes often intermingle in hibernation aggregations (Woodbury, 1951; Klauber, 1972; Gregory, 1982, 1984; Graves and Duvall, 1990), for example, it would be difficult for any male snake to track and follow, let alone guard, an individual female. Furthermore, because pitvipers are solitary hunters (e.g., Reinert et al., 1984; Duvall et al., 1985, 1990b; Hennessy and Owings, 1988; Brown, 1990a; Duvall and Chiszar, 1990; King and Duvall, 1990), it is not possible for male snakes either to guard females during prey capture or to assist females by supplying them with food. Thus, a lack of long-term female monopolization potential by male pitvipers should not lead to monogamy, as it appears to do in other animals (Thornhill and Alcock, 1983). Most snake taxa are probably similar to pitvipers in this respect. Indeed, only one squamate reptile, the shingleback skink or sleepy lizard (*Trachydosaurus rugosus*; Bull, 1988), is believed to exhibit monogamy (c.f., Parker and Brown, 1980).

Thus, most male pitvipers stand a better chance of increasing their reproductive success by searching for, locating, and successfully copulating with numerous females. Since female pitvipers can store sperm for long periods, even from matings in previous seasons (Ludwig and Rahn, 1943; Schuett, 1982, this volume; c.f., Saint Girons, 1975; Devine, 1984), and since they exhibit multiple (= mixed) paternity of clutches or litters (Schuett and Gillingham, 1986; c.f., Gibson and Falls, 1975; Schwartz et al., 1989), males will increase their reproductive success by locating and mating with as many different females as possible (c.f., Schwagmeyer et al., 1987).

But what is the ecological potential (Emlen and Oring, 1977) for local and geographic variation in pitviper mating system structure? In Figure 2 we hypothesize that the (a) temporal availability of receptive females in populations and (b) spatial distribution or predictability of receptive females, are two general factors that affect the ecological potential for polygyny among pitvipers and other snakes. These in turn must affect the probability or frequency of encounters among male and female conspecifics. With respect to temporal availability, receptive female pitvipers exhibit moderately predictable or regular populational cycles of sexual receptivity (e.g., Fitch, 1970; Klauber, 1972; Duvall et al., 1982; Saint Girons, 1982, 1985; Seigel and Ford, 1987; Duvall, under review; see below), even though periods of receptivity may be brief and explosive (as they are in many garter snakes; Gregory, 1974; Garstka and Crews, 1982; Joy and Crews, 1988; Graves and Duvall, 1990). Females may be receptive in spring, spring and late summer/fall, or late summer/fall only (e.g., Fitch, 1949, 1970; Klauber, 1972; Reinert, 1981; Diller and Wallace, 1984; Lowe et al., 1986; Schuett, this volume; c.f., Saint Girons, 1982, 1985). Local, or within-population, variation in key factors such as feeding success, thermoregulatory efficiency, and body size, likewise can affect reproductive rates and clutch sizes (Bull and Shine, 1979; Blem, 1981, 1982; Shine, 1981; Duvall et al., 1982; Diller and Wallace, 1984; Charland and Gregory, 1989; Parker and Plummer, 1987; Seigel and Ford, 1987; Graves and Duvall, 1990, under review).

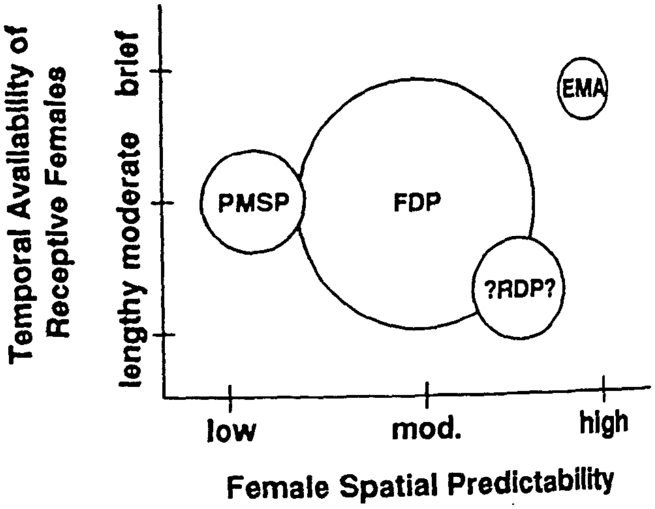

Fig. 2. Hypothesized male pitviper mating systems based upon factors affecting the temporal and spatial distribution of receptive females. These in turn likely affect probabilities or frequencies of opposite sex and conspecific encounters. FDP is female defense polygyny, RDP is resource defense polygyny (but see text for certain qualifications), PMSP is prolonged mate searching polygyny, and EMA is explosive mating assemblage. Though theoretically possible, we qualify the entry for RDP (bordered by question marks) because it has not been demonstrated in any snake. See text for discussion.

Spatial distributions of females are affected by many variables, and these, in turn, vary locally and geographically (Diller and Wallace, 1984; Reinert, 1984 a, b; King and Duvall, 1990; Duvall and Chiszar, 1990; Duvall et al., 1990a, b, unpublished data). We hypothesize that the spatial distribution of females is a general factor structuring pitviper mating systems. Associated effects appear to arise because snakes (a) are relatively slow-moving, though often wide-ranging, and highly mobile (e.g., Landreth, 1973; Shine, 1979; Brown et al., 1982; Reinert and Kodrich, 1982; Duvall et al., 1985; Gibbons and Semlitsch, 1987; Gregory et al., 1987; Macartney et al., 1988; Reinert and Zappalorti, 1988; King and Duvall, 1990), (b) are typically nongregarious and forage solitarily (Brown, 1990b; King and Duvall, 1990; Duvall et al., 1990b), and (c) they must be relatively close to conspecifics to detect their presence (e.g., within < 10 m among prairie rattlesnakes; Duvall et al., unpublished observations), unless they are following a pheromone trail (e.g., Ford and Low, 1984). Thus, factors affecting the spatial distribution of receptive females may be more important in determining local social structure in snakes than in many other animals (Ims, 1988), such as those that can detect the presence of conspecifics when they are far away (e.g., through the use of distance senses such as keen vision and audition in many birds). Fresh or nearly fresh pheromone trails may be the only class of "distance" cues that snakes regularly use to detect the moderate to distant physical proximity of conspecifics (e.g., Cowles and Phelan, 1958;

Burghardt, 1970; Chiszar et al., 1980; Brown and MacLean, 1983; Halpern and Kubie, 1984; Ford, 1986; Graves et al., 1986).

Spatial distributions of receptive female pitvipers and other snakes probably are affected by distributions of (a) food and nutrients (Arnold and Wassersug, 1978; Duvall et al., 1985, 1990b; King, 1987; King and Duvall, 1990; Duvall and Chiszar, 1990), (b) thermoregulatory or basking sites (e.g., Viitanen, 1967), (c) refugia for hibernation or estivation (Gregory, 1982, 1984), (d) temporary refugia needed for skin-shedding (Brown 1990a; Duvall, under review), and (e) areas of reduced predator abundance (e.g., Graves, 1989; Goode and Duvall, 1989). Thus, if the distribution of such factors is patchy or, more accurately, clustered (Zar, 1984; Ludwig and Reynolds, 1989), female pitvipers should exhibit a similar or equivalent distribution. If key resources are randomly or uniformly distributed, females should be similarly arrayed. However, because of the extremely high energetic costs of vitellogenesis per unit offspring, prey distributions should be especially important to females (e.g., Duvall et al., 1990a, b; King and Duvall, 1990; Duvall and Chiszar, 1990; c.f., Charland and Gregory, 1989; Graves and Duvall, 1990, under review).

ECOLOGICAL POTENTIAL, POLYGYNY, AND PITVIPER MATING SYSTEMS

Next we describe some expected pitviper mating systems (Figure 2). With minor exceptions, we follow the terminology of Thornhill and Alcock (1983). Moreover, we focus here on pattern and variation in mating success *per se,* and not on the equally important mating success-fitness covariance approach described in detail by Arnold and Duvall (under review). While only a small number of observations exist in support of the patterns displayed in Figure 2 (e.g., Fitch, 1949, 1960, 1970; Viitanen, 1967; Klauber, 1972; Gregory, 1974; Shine, 1978; Andrén, 1986; Joy and Crews, 1988; Slip and Shine, 1988; Reinert and Zappalorti, 1988; King and Duvall, 1990; Duvall, under review, see below), we nonetheless hypothesize their occurrence, based upon the rationale presented above. Furthermore, because females of many pitviper taxa and populations are seasonally variable in the number and timing of periods of receptivity as well as spatial distribution, individual populations may exhibit more than one of the following kinds of mating systems from year-to-year or even in succession within a single season. These mating systems are:

1. *Female defense polygyny* (FDP). Males actively guard or defend one or more temporarily receptive females in succession. Female defense polygyny may be the most common pitviper mating system. Sexual selection is expected to operate on male fighting abilities, mate handling, and mate persuasion traits. This form of polygyny is expected when females (a) have good spatial predictability for males, such as when and where prey are abundant and clustered, and (b) are receptive in the population for moderate to sufficiently lengthy temporal durations. This mating system may have been misidentified by squamate biologists in the past with territoriality and resource defense polygyny. Schuett and Gillingham (1989) discuss this problem.

2. *Resource defense polygyny* (RDP). Individual males compete for and defend spatial areas, called territories, that contain resources important to females (Kaufmann, 1983). Successful territory holders mate with females in these areas. Consequently, female spatial predictability is high. Asynchronous and/or lengthy periods of receptivity among females provide potential for this mating system. This social system has not been demonstrated in any pitviper or any other snake (see Schuett and Gillingham, 1989). Thus the qualification for this entry in Figure 2.

In order to verify resource defense polygyny in snakes or other organisms, the critical test is to show that (a) males compete for, occupy, and control territories, (b) females visit or occupy these areas to obtain important resources, and (c) males mate predominantly with females in these areas (c.f., Kaufmann, 1983; Stamps, 1983). Some investigators claim to have observed actions reflecting this mating system among snakes in nature (e.g., Andrén, 1986; Lowe et al., 1986). However, male-male competition for priority access to females is not sufficient alone to demonstrate this form of polygyny. In attempting to gather the needed forms of data, it will be particularly important to follow and observe continuously a focal sample of snakes in the field. Additionally, because of the seeming lack of keen distance-sensing capacities among most snakes, that would be necessary to effectively detect and potentially exclude rivals from what sometimes may be large spatial areas containing females, snakes may be constrained from exhibiting this form of social structure. Distance-sensing adaptations, such as keen vision and audition, appear characteristic of many territorial animals. Interestingly, the common adder (*Vipera berus*) studied by Andrén (1986) is apparently more "vision-dependent" during mating than many other snakes. Variable, local habitat relief, either biotic or abiotic, may constrain distance-sensing in snakes as well, especially among ground-active forms.

3. *Prolonged mate searching polygyny* (PMSP). Males search competitively for widely distributed, spatially unpredictable, and/or scarce receptive females. This is a particularly nongregarious form of animal social structure, in which frequencies of conspecific and male-female encounters are especially important (c.f., Wells, 1977). The temporal availability of receptive females in the population must at least be moderate to good, otherwise males will experience a virtual mating lottery. It is difficult to imagine how a mating lottery might evolve or remain stable in a snake system. The wide-ranging seasonal movements of many taxa are, therefore, to be expected (Brown et al., 1982; Duvall et al., 1985, 1990b; King, 1987; King and Duvall, 1990; c.f., Shine, 1979; Gregory et al., 1987; Macartney et al., 1988; Reinert and Zappalorti, 1988).

In nongregarious pitviper social systems (e.g., prolonged mate searching polygyny) seasonal encounters with conspecifics may be infrequent, especially among temperate taxa that mate late in the season and when dispersed from winter refugia (e.g., prairie rattlesnakes in Wyoming; Duvall et al., 1985; King and Duvall, 1990; Duvall, under review; c.f., King et al., 1983). Accordingly, little male-male fighting should occur if for no other reason than males will only rarely find themselves in the simultaneous presence of other males and a receptive female. Thus, any potential sexual by males will be greater than those for females, again so long as there is some variation in female mating success.

Operational and Breeding Sex Ratios

As noted above, male-biased OSRs have been hypothesized to give rise to various forms of male-male competition that in turn may generate sexual selection forces acting on males. Accurate OSRs (i.e., the ratio of the number of available males/number of available females) are often difficult to measure or estimate (e.g., Kluge, 1981; King and Duvall, 1990). Additionally, Ims (1988) demonstrated that female- more so than male-biased OSRs increase variance in male mating success, in mating systems characterized by male mate searching and/or fighting. This finding runs counter to predictions of Emlen and Oring (1977). Thus, the general predictive utility of OSRs in empirical work may be less than most investigators would desire. Although the BSR also may be difficult to measure directly in field studies of snakes, to the extent that it at least can be estimated it may tell us more than the OSR about potential sexual selection forces operating on males and females. As noted above, we define BSR as the ratio of the number of actual male parents/number of actual female parents. Arnold and Duvall (under review) find that the ratio of the male to female sexual selection gradients (e.g., from equations 3, 4, and 5) equals the squared BSR. Likewise, BSR equals the ratio of male to female mate cycling coefficients (α; see equations 6 and 8 below). Thus, to the extent that the BSR or its components can be measured or estimated accurately, and to the extent that the assumptions of the encounter rate model apply (Arnold and Duvall, under review), this value can provide one accurate index of the ratio of sexual selection gradients/forces acting on male and female mate encounter and handling rates. In many snake systems, it is possible to estimate or determine the actual numbers of female parents accurately and reliably (e.g., King, 1987; Charland, 1989; Macartney and Gregory, 1988; Graves and Duvall, 1990, under review). The number of breeding males is more difficult to estimate, but molecular techniques such as protein electrophoresis and DNA fingerprinting could be employed (e.g., Crabtree and Murphy, 1984; Gibbs et al., 1990). Numbers of male parents can beestimated indirectly from certain components of the BSR value as well.

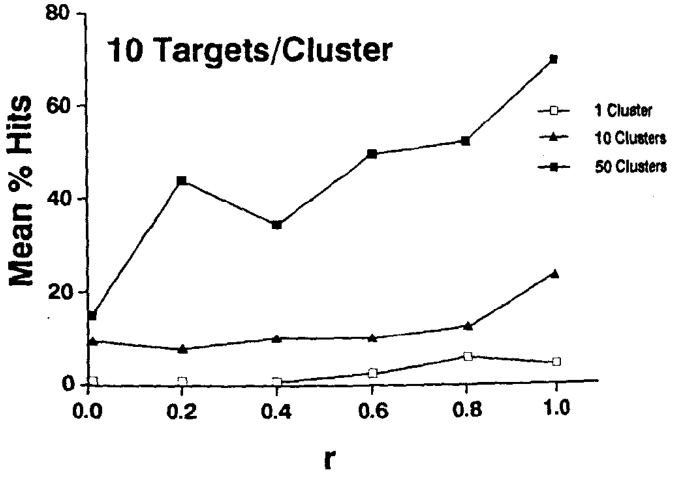

Fig. 5. Results from several runs (n = 360 for each data point) of the spatial searching simulation RattleSnake© (Duvall et al., 1989, 1990a, under review; Mintzer et al., 1992). Regardless of cluster number (1, 10, or 50), when resource units or targets are spaced in this way (i.e., when the mean is less than the variance in the frequency of targets per constituent unit space; Ludwig and Reynolds, 1989; Zar, 1984), two dimensional search paths of high angular fixity, vector magnitude (r; Batschelet, 1981), or straightness, generate the highest hit rates or collisions with targets. Thus, males searching for spatially clustered females should follow paths of high r. As discussed in the text, when searching for clustered targets of unknown location, maximizing r will minimize searching duration (s).

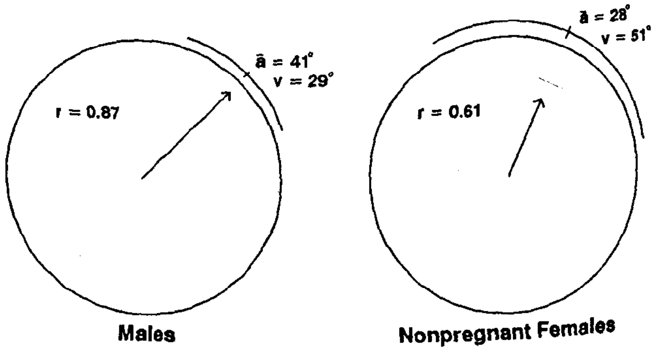

Fig. 6. Vector magnitudes (r), average angles of dispersion from the den ($\bar{a}$), and a measure of angular variation (v), for vernally migrating male and nonpregnant (sexually receptive) female prairie rattlesnakes, studied in 1982 and 1984. The statistics r, $\bar{a}$, and v are not included in Table 1. These diagrams are modified from King and Duvall (1990). Vector magnitudes of males are significantly straighter, or spatially more efficient (given the clustered distribution of prey patches), than those of females (King and Duvall, 1990). Perhaps even the vernal foraging movements of males are under the influence of sexual selection forces acting to minimize α_s in a prolonged mate searching polygynous mating system. See text for discussion.

An Encounter Rate Approach

Several investigators have developed predictive models to study expected and observed encounter rates with needed resources, such as potential mates (e.g., Holling, 1959; Parker, 1970, 1978; c.f., Cox, 1962; Stephens and Krebs, 1986). Implicit in some of these approaches is the assumption that the relative encounter rate with potential mates comprises a major difference between the sexes (e.g., Baylis, 1981; Parker, 1970; Sutherland, 1985 a, b). Sutherland (1985 a, b, 1987) has presented some interesting encounter rate models dealing with mate searching (s) and handling (h), and sexual selection, derived from certain components of renewal theory (Cox, 1962). Sutherland only allowed s to follow a Poisson distribution, and h was not allowed to vary at all. Such an approach may have limited utility for investigators studying variable organisms inhabiting a variable world. However, Sutherland did include a small number of discrete levels of a factor reflecting the ability of males to find females (i.e., "Parker's aptitude for encounter"). And as is in many encounter rate models, Sutherland assumed that all partners encountered and handled are mated successfully.

We have developed a set of encounter rate predictions, likewise derived from renewal theory, that allow s and h to assume arbitrary, independent statistical distributions

(Cox, 1962). Additionally, since not all potential mates encountered and handled actually will mate, we incorporate a measure of mate persuasion, p, with an index of average mate persuasion, α_p. This parameter equals the average proportion of mates located and handled that are successfully mated (see equations 6, 7, 8, and 9 below). Following Sutherland (1985 a, b, 1987), we also assume that during a mating season of duration L, a male spends all of his time either searching (time s) for or handling (time h) mates. Handling includes activities such as mate accompaniment, mate guarding, courtship, and male-male fighting. Males and females can have different characteristic mating periods, L. In prairie rattlesnakes, for example, females never have been observed to search for male mates (King, 1987; King and Duvall, 1990; Duvall, under review).

Thus, focusing on males, for example, we find that average mating success is

$$\bar{X}_m = \alpha_p L/(\alpha_s + \alpha_h), \qquad (6)$$

where α_s and α_h are the means for search and handling times, and sum to equal average mate cycling time, α. Variance in mate cycling time is given by σ^2. Thus, males can increase mating success by (a) increasing persuasion abilities, or the average proportion of mates encountered and handled that are mated successfully, (b) maximizing the length of the mating season, and/or (c) decreasing mate cycling time (c, where c = s + h) needed to search for and handle successive mates. Variation in male mating success ($\sigma^2_{x\text{-}m}$), and, hence, potential sexual selection (see Arnold and Duvall, under review), is increased by all those factors that cause intrinsic differences among males in (a) searching and handling, and, thus, mate cycling times, (b) the duration of mating seasons, and (c) mate persuasion abilities. Specifically, we find that

$$\sigma^2_{x\text{-}m} = (\alpha^2_p L^2/\alpha^2)\ \{ (1/\alpha L)\ \sigma^2 + (1/\alpha^2_p)\ \sigma^2_p\}. \qquad (7)$$

Thus, variance in male mating success will be increased by (a) high mate persuasion efficacy, lengthy mating season durations, and brief mate cycling times, (b) enhancing effects of brief mate cycling and short mating seasons on variance in mate cycling, and (c) enhancing effects of low average persuasion on variation in this parameter. Arnold and Duvall (under review) address the issue of standardized variance (to a mean of one) in mating success, I_s, often considered to be a useful index of the opportunity, or potential, for sexual selection (e.g., Crow, 1958; Wade and Arnold, 1980; Arnold, 1986), from the encounter rate and persuasion approach presented here.

These predictions appear to have direct relevance to studies of pitviper mating systems (see below). Furthermore, RattleSnake© (Duvall et al., 1989, under review; Mintzer et al., 1992) can be used to test some of these predictions, especially those affected by spatial variables, and, thus, to generate even more refined predictions for empirical tests in nature.

It is also useful to cast this encounter rate approach in terms of sexual selection gradients. By calculating the partial derivative of $\bar{X}_m$ with respect to α_s and α_h, we find that

$$\beta ss\text{-}\alpha_s = \beta ss\text{-}\alpha_h = \beta ss\text{-}\alpha = -\alpha_p L/(\alpha_s + \alpha_h)^2 = -\alpha_p L/\alpha^2, \qquad (8)$$

and for α_p,

$$\beta ss\text{-}\alpha_p = L/\alpha. \qquad (9)$$

Consequently, sexual selection on male rates is expected to increase as (a) average persuasive abilities increase, (b) the duration of mating seasons or periods increase, and/or (c) average mate cycling times decrease. Sexual selection should act on males to (a) increase persuasive abilities, (b) increase the duration of mating periods, and (c) decrease the duration of average mate cycling times. In general, sexual selection on rates should be most intense when α_p and L are much greater than α. Additionally, sexual selection on male persuasive abilities should increase as the mating season lengthens and mate cycling times decrease.

Predictions of this nature appear testable, and raise some interesting possibilities for the kinds and combinations of traits that sexual selection forces should favor. In our prairie rattlesnake system, for example, L is limited by the rate and periodicity of the female reproductive cycle; males have no control over the absolute duration of the single, mid-to late-summer mating window (King and Duvall, 1990; Duvall, under review). Conversely, male encounter rates with females are low on our site (see below), suggesting that suites of traits associated with movement, locomotion, efficient foraging, orientation and navigation, speed and endurance, mate location, or traits associated with α_s in general, may be under intense sexual selection. Likewise, because receptive females are encountered rarely in this system (see below), sexual selection especially should favor minimization of failed mating opportunities by males when mates are located; that is, sexual selection should favor increased mate persuasion efficacy. When ecological potential gives rise to spatial and temporal distributions of female pitvipers that are more predictable than in Wyoming (Figure 2), male-male fighting may be more common and, in turn, associated with increased sexual selection on any number of handling time-related traits. Generally, sexual selection might operate to minimize the duration of events related to α_h when receptive females are more predictable in space and time.

PROLONGED MATE SEARCHING POLYGYNY IN PRAIRIE RATTLESNAKES

In the course of a long-term study of the biology and behavior of radiotagged, free-ranging prairie rattlesnakes in the Haystack Mountains of the high, cold Red Desert of southcentral Wyoming (see references by D. Duvall, M. B. King, B. M. Graves, and associates), Duvall (under review) simultaneously observed and monitored a number of indices and correlates of potential male and female mating success. See Duvall (under review) for a more thorough discussion of these findings; they only are summarized here.

Although we have tracked and observed over 100 radiotagged snakes for much of their active season during eight successive years of fieldwork, the numbers of individual males and females that were followed on daily (or continuous) bases are much smaller. These kinds of data, derived from daily tracking of individuals for entire seasons, are critical to analyses of mating success and mating systems. For example, if we lost track of a snake for, say, a week, then we would have no knowledge of whether or not the animal mated during this period. Thus, complete and continuous records of encounters between *individual* males and females across entire seasons are critical. Because prairie rattlesnakes selection that might operate should act on (a) searching and mate location traits, more so than fighting abilities, and (b) efficient handling and persuasion of receptive females once located.

4. *Explosive mating assemblage* (EMA). Males in large groups literally "scramble" to successfully mate with either fairly scarce or abundant females, that are nevertheless closely clustered in space and exhibit a brief period of sexual receptivity. The best examples in snakes are temperate populations of communally denning garter snakes (e.g., *Thamnophis sirtalis* and *T. elegans*), where males emerge from hibernation before females and wait at the den entrance for spring breeding females to emerge (e.g., Gregory, 1974; Joy and Crews, 1988; Graves and Duvall, 1990). Instantaneous OSRs may be strongly male-biased in these circumstances (Gardner, 1955; Gregory, 1974), as small numbers of emerging females are deluged by large numbers of sexually primed males that have emerged earlier. Not surprisingly, male-male sexual interference has been observed among garter snakes in these circumstances. Mating plugs are formed during copulation, that may interact to reduce female attractiveness (Ross and Crews, 1977), presumably to enforce first-male advantage and female chastity (Devine, 1977, 1984; but c.f., Gibson and Falls, 1975; Schwartz et al., 1989). Female pheromone mimicry by males ("she-males") even has been reported in some populations of garter snakes, perhaps reflecting yet another form of male-male sexual interference (Mason and Crews, 1985). Pitvipers that hibernate or even estivate in small to moderate numbers (e.g., Fitch, 1970; Klauber, 1972; Lowe et al., 1986), and that mate upon emergence, might be hypothesized to exhibit explosive mating assemblages as well. However, and as noted above for temperate taxa that hibernate in large numbers at overwintering dens, mating at spring emergence may be less common than has been previously hypothesized (King and Duvall, 1990; Schuett, this volume).

Potential actions of sexual selection in explosive mating assemblages are probably complex. Because so many males appear to be struggling with each other for mating success, sexual selection could be generated through these interactions. A large fraction of the males in these scrambles will experience mating failure. Mating failure is a primary factor affecting variation in mating success and the potential intensity of sexual selection among all sexually reproducing organisms (see below). In *T. sirtalis*, Joy and Crews (1988) have shown that variation in male body size does not contribute significantly to variation in male mating success in explosive mating assemblages. Perhaps sexual selection operates on male agility and endurance instead. Given the hypothesized existence *a priori* of this mating system in wandering garter snakes (*T. elegans vagrans*) in Wyoming, Graves and Duvall (1990; c.f., Gregory, 1974) predicted and observed that sizable numbers of males emerged from winter hibernation significantly sooner than females, presumably to secure a mating.

Finally, and though theoretically possible, we know of no reports of active mate choice by any female snake and, thus, omit *Lek polygyny* (see Emlen and Oring, 1977; Thornhill and Alcock, 1983; Vehrencamp and Bradbury, 1984; Wells, 1977). In this social system, males compete for display territories that contain no key "resources" for females, that is, other than the *presumptive* "good genes" of superior males (see Arnold, 1983, 1985; Halliday, 1983; Kirkpatrick, 1987). It is hypothesized that females come to Leks in order to select mates.

A MICROEVOLUTIONARY AND ENCOUNTER RATE APPROACH TO SNAKE MATING SYSTEMS

As noted above, most variation in the form of snake polygyny and mating systems probably is generated by variation in male and not female mating strategies. Thus, what are the forces that shape the mating tactics of males? Several relevant and helpful contributions exist along these lines (e.g., Bateman, 1948; Crow, 1958; Parker, 1970, 1978; Payne, 1979; Wade, 1979; Alcock, 1980; Arnold and Wade, 1984 a, b; Sutherland, 1985 a, b; 1987; Endler, 1986; Ims, 1988; c.f., many contributions in Bateson, 1983, and Bradbury and Andersson, 1987). Nevertheless, additional general but precise quantitative approaches would be helpful. Our goal at this point is to summarize components of a quantitative selection theory, encounter rate, and mating success approach to analyzing animal mating systems and sexual selection developed by Arnold and Duvall (under review). Our concern here is with how these approaches might give rise to predictions about pattern and variation in snake reproductive strategy. Additionally, though Arnold and Duvall (under review) address the complicating issues of population age-structure and mortality on mating success-fitness and sexual selection gradients, we do not take these issues up here. Rather, herein we focus on seasonal, or cross-sectional, approaches to snake mating system analysis. Future efforts profitably might take age-structuring and mortality issues into account.

As observed by Bateman (1948), males should often exhibit greater variation in mating success than females (Figure 3). While it may be inappropriate to view this variation as the cause of sexual selection (Sutherland, 1985 a, b, 1987), and while random variation may explain some of Bateman's conclusions (c.f., Sutherland, 1985 a, b, 1987), Bateman's observed sex differences in variance in mating success do reflect the operation of sexual selection (Wade, 1987; Arnold and Duvall, under review). Indeed, Bateman's (1948) work has fundamental significance for analyses of sexual selection and pitviper mating systems. Arnold and Duvall (under review) propose that regressions of fitness (number of offspring) on mating success (numbers of mates), for both males and females, may be thought of as sexual selection gradients (Lande, 1979; Wade and Arnold, 1980; Lande and Arnold, 1983; c.f., Arnold, 1983, 1985) reflecting the final common pathway through which all sexual selection forces must operate. In the case of Bateman's flies, the sexual selection gradient for males has a greater slope than that for females (Figure 3). These gradients would be expected to be the reverse in polyandrous taxa (Arnold and Duvall, under review). Thus, a key to understanding mating systems of snakes or any other kind of sexually reproducing organism is to focus on the number of mates that actually produce progeny, not mating success alone.

The modeling of snake mating systems based upon the notion of a mating success-fitness final common pathway

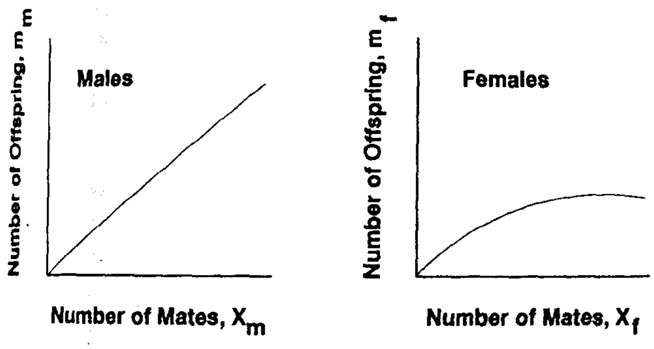

Fig. 3. Regressions of fitness or the number of offspring (for males and females, m_m and m_f, respectively) on mating success or the number of mates (again for males and females, X_m and X_f, respectively), modified from Bateman (1948). These regressions can be thought of as gradients representing the final common pathway through which sexual selection forces operate on traits (Arnold and Duvall, under review). Male and female pitvipers probably are similar to other polygynous organisms in these respects. See text for discussion.

for sexual selection forces leads to some potentially interesting predictions. We focus here on those predictions relevant to pitvipers (and, perhaps, other snakes). Variables discussed below are summarized in Table 1.

First, imagine a population in which males may mate with multiple females and can realize increased fitness (= fecundity or progeny count) from these multiple matings. Females, conversely may mate repeatedly, once, or not at all, but realize no increased fitness beyond that derived from the first mating. In other words, the expected fitness of a female is zero if she fails to mate and it is some constant, say $\bar{m}_f$, if she mates once or more. This relationship likely exists in many pitviper populations (see below). Under this system the expected fitness ($\bar{m}_m$) of a male is

$$\bar{m}_m = \bar{m}_f \bar{X}_m, \qquad (1)$$

where $\bar{X}_m$ is the average male mating success (= the number of females mated). Though open to other interpretations, Crabtree and Murphy (1984) describe allozyme data from a natural population of prairie rattlesnakes which suggest that entire litters from three individual females had single sires. More data on numbers of copulations and successful matings by free-ranging female pitvipers are sorely needed (but see below). Nevertheless, as demonstrated by several investigators (e.g., Schuett and Gillingham, 1986; c.f., Gibson and Falls, 1975; Saint Girons, 1975; Schwartz et al., 1989), female snakes may store sperm from multiple matings and produce clutches or litters of mixed paternity. Therefore, if we assume that the number of progeny sired by a male is inversely proportional to the number of males mated by a particular female, then expected male fitness becomes

$$\bar{m}_m = (\bar{m}_f/H_x)\,\bar{X}_m, \qquad (2)$$

where H_x is the harmonic mean mating success of females with one or more mates (see Figure 4). We assume no mating order effects among potential sires (but see Dewsbury and Baumgardner, 1981; Schwagmeyer et al., 1987). The physiological mechanisms mediating potential multiple paternity of clutches in the squamates is unknown (e.g., Schuett, this volume). In neither of the above *single or multiple male paternity mating systems* do we assume (a) any parental care of offspring or (b) presentation of nuptial gifts to the female by a male (such as an energy-rich spermatophore; e.g., Thornhill and Alcock, 1983; Gwynne, 1991).

By calculating the first derivative of average male fitness ($\bar{m}_m$) with respect to average mating success ($\bar{X}_m$), we find that the sexual selection gradient for males ($\beta_{ss\cdot m}$; reflecting the direct force of directional selection; e.g., Lande and Arnold, 1983; Phillips and Arnold, 1989), in a system of single male paternity for females, is

$$\beta_{ss\cdot m} = \bar{m}_f. \qquad (3)$$

Under a system of multiple female mating with multiple male paternity this gradient becomes

$$\beta_{ss\cdot m} = \bar{m}_f/H_x. \qquad (4)$$

Thus, multiple mating by females coupled with multiple paternity is expected to reduce the intensity of sexual selection on males. In populations and taxa where the latter mating system is characteristic, male-male competition likewise might be less pronounced.

Again, though not likely to be relevant in considerations of most snake mating systems, it is nevertheless useful to specify expected sexual selection gradients for females and the factors that may affect them (c.f., Arnold and Duvall, under review). This is because males and females, and the reproductive success they realize, are bound or coupled by the BSR (see below). It can be shown, for example, that average male mating success ($\bar{X}_m$) equals average female mating success ($\bar{X}_f$) divided by the BSR (Arnold and Duvall, under review). The factors affecting female sexual selection gradients are somewhat more complex than for males. We find that the sexual selection gradient for females ($\beta_{ss\cdot f}$) is

$$\beta_{ss\cdot f} = q\bar{m}_f\,\bar{X}_f/\sigma^2_{X\cdot f}, \qquad (5)$$

where q equals the proportion of females capable of breeding that do not, and $\sigma^2_{X\cdot f}$ is the variance among all females in mate number (including the zero class with no mates). Thus an important factor increasing sexual selection forces acting on females is mating failure, so long as there is some variation in female mate number. This effect of mating failure on female sexual selection gradients parallels a similar general situation for males. Nevertheless, since the number of capable but nonbreeding females in populations of most species is expected to be small (e.g., Darwin, 1871; Bateman, 1948; Parker, 1984; Trivers, 1972), q likewise becomes small and $\beta_{ss\cdot f}$ approaches zero. If all capable females breed, then sexual selection gradients experienced

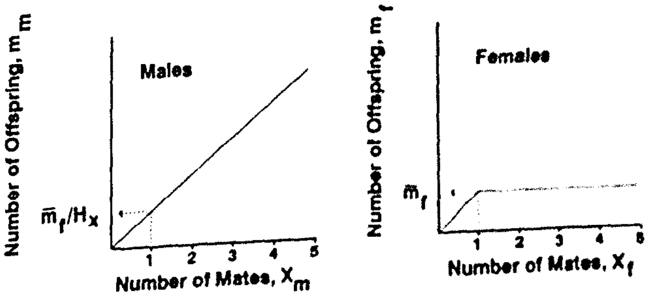

Fig. 4. A system where average female fitness ($\bar{m}_f$) does not increase after the first mating, but where male fitness ($\bar{m}_m$) does. However, for multiple sires and mixed paternity of broods, with no mating order effects, average male fitness will decline as a function of the harmonic mean number (H_x) of male mates per individual female (e.g., $\bar{m}_f/H_x$). See text for discussion.

and other pitvipers are long-lived, late-maturing, and iteroparous (e.g., Parker and Plummer, 1987), it would be ideal to have data for individual mating success and even fitness across the lifespan (e.g., Howard, 1983; Clutton-Brock, 1988; Arnold and Duvall, under review). However, it may be some time before remote tracking methods (e.g., radiotelemetry) are available that allow continuous study of individual snakes for lengthy durations. Nevertheless, and as noted above, Arnold and Duvall (under review) take up at least one set of approaches that address effects of age-structuring and mortality variables.

Accordingly, we summarize here cross-sectional data derived from 24 males and 17 nonpregnant (= receptive) females, tracked and observed on daily bases for entire durations of single seasons. Most of the observations we discuss were collected in 1984, and 1986 through 1988. One data set derives from a male tracked in 1982.

Continuous and long-term tracking of individuals was necessary to characterize accurately (a) the duration of the mating season and period of female receptivity (c.f., Duvall et al., 1985; King and Duvall, 1990), (b) ecological potential for prolonged mate searching polygyny (c.f., Duvall et al., 1985; 1990b; Duvall and Chiszar, 1990; King and Duvall, 1990), (c) indices of variation in potential mating success among males and females, and (d) variation in key phenotypic traits hypothesized to be associated with mating success. [See King and Duvall (1990) and Duvall et al. (1990b) for reference to radiotag surgical implantation procedures and related details. Generally, we adhere to the procedures and recommendations of Reinert and Cundall (1982). Radiotag to snake body mass ratios, expressed as percents, were ca. 7 % in 1982 and 1984, and ca. 3 % in 1986 through 1988.]

Duration of the Female Mating Season

Though much confusion has surrounded the precise duration and periodicity of cycles of pitviper sexual receptivity in nature (but see Fitch, 1970; Klauber, 1972; Seigel and Ford, 1987; Schuett, this volume), the only way to answer these questions conclusively is to track and observe free-ranging individuals and describe the numbers and kinds of relevant sexual interactions that occur. In samples comprised of ca. 100 radiotagged males and nonpregnant females (and via anecdotes derived from observations of hundreds of nontagged individuals; e.g., Graves and Duvall, 1990), we have observed the following events to occur solely between the period early July and late August and never at the den entrance: (a) *Accompaniment*, or close tracking and near-continuous physical contact by a male with a receptive female, that lasts typically from 2 to 4 days prior to courtship and copulation. Some period of accompaniment always precedes courtship and copulation. Thus, accompaniment is an excellent index of mate location and potential mating success among males. It is a similar index for females, except that it reflects having-been-located. We never have observed any action on the part of females on our site that might be construed as mate searching or mate choice. Females appear to be oblivious to males, except during actual courtship and copulation. Additionally, animals destined to become sexually active in a particular season are completely solitary and nongregarious, exhibiting no accompaniment from hibernation emergence in May through the onset of mating activities in early July (King and Duvall, 1990; Graves and Duvall, under review; c.f., King et al., 1983). (b) *Courtship* involves chin-pressing and rubbing, body-rubbing, and the delivery of many rapid and short tongue flicks by a male to the female's dorsum, as well as cloacal apposition, and attempts at intromission (Duvall et al., 1985; Hayes et al., 1991; c.f., Gillingham, 1987; Schuett and Gillingham, 1988). We have observed entire and partial courtship sequences in eight and ca. 23 male-female pairs, respectively. (c) *Copulation* is recognized as occurring from the moment of successful intromission, during a copulatory lock, and through termination of coitus. In the eight matings observed and scored to completion or termination of coitus, the average duration of copulation, as we have defined it, was ca. 90 minutes (Duvall et al., 1985; but c.f., Klauber, 1972; Schuett and Gillingham, 1986). Upon termination of coitus, pairs broke up and individuals moved apart. Males will accompany a new female within a few days of coitus. Females, conversely, remain unaccompanied for a week or two at a minimum, and sometimes for the remaining duration of the season, subsequent to a previous accompaniment. Duvall (under review) discusses these trends in more detail. In the Sand Hills of Nebraska, where growing seasons and summer average daily temperatures are much greater than those experienced by snakes in the Haystack Mountain population, A. Holycross (pers. comm.) has observed commonly spring mating in prairie rattlesnakes. This pattern is consistent with certain predictions inherent in Figure 1. regardless, our observations of males in Haystack Mountain prairie rattlesnake populations indicate a mid- to late-summer mating window of ca. seven weeks in duration, which corresponds exactly to the period of female receptivity. In terms of Figure 2, we view this as reflecting moderate to good temporal availability of receptive females. As observed by King and Duvall (1990), and discussed by Duvall (under review), the period of female receptivity commences immediately subsequent to a mid-summer skin-shedding event among those females destined to mate in any particular season. Sex pheromone production probably is associated with the skin and skin-shedding (e.g., Kubie et al., 1978; Gillingham and Dickinson, 1980; Garstka and Crews, 1981, 1982; Ford, 1986; Gillingham, 1987; Mason et al., 1989; Weldon et al., this volume).

G. Schuett and H. Austin (unpublished data) have found that male prairie rattlesnakes in Haystack Mountain populations emerge from hibernation in the spring with regressed testes but large quantities of fully developed and motile sperm throughout the ductus deferens. Nevertheless, no spring mating occurs in these populations (c.f., Rahn, 1942; Ludwig and Rahn, 1943; King and Duvall, 1990). Thus, the timing and duration of the period of female receptivity, rather than the spermatogenic cycle, appear to be major factors driving local mating system structure (Garstka and Crews, 1982). In more southerly populations of this subspecies (Klauber, 1972), just as in Nebraska, (A. Holycross, personal communication), where food and warmth may be more abundant (e.g., parts of Colorado, New Mexico, Texas, Oklahoma, and Mexico), perhaps females mate upon spring emergence and even close to entrances of overwintering refugia (Fitch, 1949; c.f., Solórzano and Cerdas, 1989). They likewise may exhibit another window of receptivity late in the summer. This hypothesized pattern seems possible because of the well-known stimulatory effects of warmth on rates of reproductive cyclicity among the squamates (e.g., Duvall et al., 1982; Figure 1). If females in southern populations are receptive upon spring emergence, then the expected mating system should be female defense polygyny or explosive mating assemblage. If they become receptive only once, or for a second time late in the summer, and long after individuals have dispersed from dens, one of the other forms of polygyny described above may be characteristic (Figure 2). Saint Girons (1982, 1985), Seigel and Ford (1987), and Schuett (this volume) discuss the temporal sequencing of snake reproductive cycles.

Spatial Ecological Potential

Deer mice (*Peromyscus maniculatus*), the most commonly occurring and favored prey of Haystack Mountain prairie rattlesnakes, are sparse in numbers, spatially unpredictable, and widely distributed (Duvall et al., 1985, 1990b; King, 1987; King and Duvall, 1990). Deer mouse patches, usually ca. 50 m in diameter are, in a strict sense, highly clustered or contagious in spatial distribution. Such contagion is characterized by a variance that exceeds the mean (Zar, 1984; Ludwig and Reynolds, 1989). Females spend entire active seasons foraging and thus moving between the sparse and widely-dispersed deer mouse patches at our site. Males, conversely, search for two different types and sets of clustered targets per season; deer mouse patches in the first half of the summer and receptive females in the second (King and Duvall, 1990; c.f., Reinert and Zappalorti, 1988). It should be noted, however, that an adult prairie rattlesnake probably consumes fewer than ca. five-eight deer mice per season (King and Duvall, 1990; c.f., Mushinsky, 1987; Diller and Johnson, 1988).

Thus, the spacing of deer mouse patches will generate associated distributions of receptive females come mid-summer, which in turn creates the local ecological potential for prolonged mate searching polygyny. We may ask, therefore, how best to locate patches or targets that are few, widely distributed, and clustered in space, when the searcher (a) moves slowly, (b) has a short season in which to locate resources targets, and (c) requires only one or a few successful "collisions" with the target? As hypothesized by Duvall et al. (1985), the computer simulation model RattleSnake© (Mintzer et al., 1992) shows us that search paths of high vector magnitude (i.e., two dimensional paths that are highly straight in shape), will maximize the likelihood of collisions with clustered targets of unknown location. Conversely, search paths approaching a random walk will minimize the probability of collisions. Figure 5 summarizes some results of a simulation employing Haystack Mountain-type parameters for searching rattlesnakes (Duvall et al., 1989, under review; c.f., Duvall et al., 1990a, b). Interestingly, Duvall et al. (1985) and King and Duvall (1990; Figure 6) report vernal search movements of significantly greater vector magnitude among male as opposed to female prairie rattlesnakes. This sex difference in spatial searching efficiency (King and Duvall, 1990) may reflect the fact that males must search for twice as many stations or kinds of targets per season than do females (Baker, 1978; c.f., Gaulin and Fitzgerald, 1986). Clearly, rodent and associated female spatial distributions in the Haystack Mountains generate the ecological potential for a highly mobile and nongregarious, search-based mating system. Of particular relevance to issues discussed here, however, is the prediction (equation 6) that males may maximize mating success by minimizing search, and, thus, cycling time. Indeed, because so many males fail to locate even a single female (see below), seasonal male mating failure must be be quite high. Thus sexual selection may be so intense in this population as to affect any number or combination of traits that may act directly or indirectly to minimize α, and, more specifically, α_s. For example, perhaps male foraging patterns and spatial efficiency during the first half of the summer are affected by some sexual, as well as natural, selection forces, even though the mating season comprises the second half of the summer. Generally, a clear-cut and convenient partitioning of natural and sexual selection forces in competitive search-based mating systems may be less straightforward than in mating systems affected by male-male fighting or female choice.

Variation in Male and Female Mating Success and Failure

For many of the reasons enumerated above, we have hypothesized that male prairie rattlesnakes would exhibit greater mating failure and variation in mating success than females, reflecting the potential operation of sexual selection. This is precisely what has been observed. Note that alpha = 0.05 for all effects referred to here as significant.

Of the 24 males and 17 females that were radiotagged, and tracked and observed on daily bases for entire seasons, 10 (42%) and 14 (82%), respectively, were observed in mating accompaniment with one or more different mates. Thus slightly less than one half of the males located even a single potential mate during study seasons. Additionally, since some period of accompaniment always precedes courtship and copulation, we consider accompaniment to be an accurate index of mate location by males. Since males obviously must locate females in order to mate with them, accompaniment likewise can be considered an index of potential mating success.

We observed that 14, 6, 3, and 1 males were in accompaniment with 0, 1, 2, and 3 different females, respectively. Three, 4, 4, 4, and 2 females were observed in accompaniment pairs with 0, 1, 2, 3, and 4 different males, respectively. Thus, for males, we find a Poisson-like distribution of accompaniment or potential mating success, reflected in: mean = 0.63, standard deviation = 0.88, variance = 0.77, range = 0-3, and skewness = 1.20. Conversely, among females we observe a more uniform distribution of potential mating success or accompaniment, in turn reflected in: mean = 1.88, standard deviation = 1.32, variance = 1.74, range = 0-4, skewness = 0.51. Thus from accompaniment data, the opportunity for sexual selection, I_s (the variance estimate I_s = $s^2/\overline{x}^2$, standardized to a mean of *one*; Crow, 1958, 1986; Arnold and Wade, 1984 a, b; Trail, 1985; Wade, 1987; Wade and Arnold, 1980) for males and females, equals 1.94 and 0.48, respectively. Thus, the high level of potential mating failure among males, as estimated from accompaniment data, increases the standardized variance in potential mating success and, in turn, enhances the opportunity for sexual selection. A two-sample, Kolmogorov-Smirnov test for inequality of distributions (Zar, 1984), also indicates that the two distributions are different. A simple comparison of sex differences in proportions of mating failure likewise indicates the presence of a significant difference. Duvall (under review) discusses these various estimates. Kluge (1981) provides a good general discussion of appropriate variance estimates for mating success data.

Because of commitments to other projects while these data were being collected, we were unable to remain with each accompaniment pair to verify that a successful copulation had been accomplished. Future studies of a more time-intensive nature are needed to fill in the many gaps in our data set. It is particularly important to learn, for example, how many times females successfully mate per season. Such data will be especially important to attempts to measure or estimate mate persuasion, p. Nevertheless, because all of the courtships and copulations that we have observed occur subsequent to at least one full day of accompaniment, we are confident that the latter variable is positively associated with efficacious mate handling and copulation. Duvall (under review) discusses the positive associations between accompaniment, courtship, and copulation.

Regardless of the positive correlation between male accompaniment and copulation, however, is the fact that accompaniment is an extremely accurate measure of mate location in our system. Males located an average of only 0.63 females per season. Females, in turn were located by an average of 1.88 different males per season. These values indicate a low frequency of conspecific encounters per active season, reflecting the nongregarious nature of this rattlesnake mating and social system. Thus, data accurately reflecting the number of times that males and females locate or encounter potential mates have considerable utility.

As hypothesized, fighting was infrequent, as two or more males were rarely observed in the simultaneous presence of a receptive female. To date we have observed five fights on our site.

Some Traits Associated with Potential Mating Success

Sutherland (1985 a, b, 1987) has demonstrated that random rather than deterministic effects can account for meaningful components of variation in mating success. Statistical regression of mating success on relevant phenotypic traits is one way to separate deterministic and stochastic components, however. Duvall (under review) has calculated some univariate regressions of male and female accompaniment on several key phenotypic traits. We only summarize some of these findings here. All of the traits considered among males, for example, were related in some way to movement and body size. These included regressions of accompaniment on (a) body mass to snout-vent length (size) residuals, (b) number of season-long movements, (c) number of movements during the mating season, (d) rate of season-long movement, (e) rate of mating season movement, (f) accumulated time needed for mid-summer skin-shedding, and certain others. While some were found to be significant (e.g., number of mating season movements, minimizing the duration of skin-shedding), others were not (e.g., body size residuals). It appears, therefore, that some deterministic sexual selection operates on certain movement-related traits among male prairie rattlesnakes in the Haystack Mountains. Some of these traits appear to be employed to utilize efficiently the time available to males in mate searching during period L (e.g., minimizing the time required for mid-summer skin-shedding). Many of these effects are consistent with the hypothesized general picture of (a) potential competitive male mate searching, (b) prolonged mate searching polygyny, and (c) a nongregarious social system, in this population of pitvipers.

Although Duvall's (under review) observations of free-ranging prairie rattlesnakes may suggest some possible directions for future studies of snake mating systems, the data set is less than ideal. First, it is much too small. Larger data sets are needed, for example, in order to study multivariate selection. Second, it would be especially useful to have data on copulatory and not just mate location success. If such data were to become available, it would facilitate accurate measurement or estimation of mate handling and effective persuasion. Third, it would be particularly useful to have more data on individual fitness, both derived from season-long (cross-sectional) and, more preferably, longitudinal (several seasons or even complete lifespans) observations. And last, it also would be useful to attempt relevant field experiments (e.g., Andersson, 1982; Duvall et al., 1990b).

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