

The Greenhouse Effect and Changes in Animal Behavior: Effects on Social Structure and Life-History Strategies

DANIEL I. RUBENSTEIN

I. INTRODUCTION

The primary purpose of this chapter is to review selected examples of animal behaviors, such as feeding or reproduction, that vary with climate and therefore are likely to change substantially if global warming occurs. Because these behaviors are closely tied to survival and reproduction, many changes in behavior may have substantial ecological and evolutionary repercussions. Changes in mating behavior, for example, may alter the genetic structure and demography of populations. Behavior likely to have ecological and evolutionary consequences will be the focus of this chapter.

Since adjusting behavior is often an animal's first means of coping with changing environmental conditions, climatic changes wrought by the greenhouse effect should change substantially the quality or frequency of many behaviors. Indications of possible future changes can be observed when seasonal or other short-term changes in temperature or rainfall cause animals to alter their ranging, feeding, and mating behavior. Thus, a drop in temperature often induces small mammals to change their activity patterns, spending more time huddling, while a short-term decline in food abundance often causes foragers to spend less time searching in particular patches (Krebs and Davies 1987).

The problem of projecting future behavioral changes is complicated because only some of the effects of climate change will directly affect behavioral response. Many other effects will be indirect and therefore harder to predict. For example, large mammals, such as elephants, horses, and topi, respond to changes in landscape pattern induced by climatic changes. Similarly, ecological stresses that change the balance between adult and juvenile mortality may change reproductive strategies and thus reproductive behavior (Horn and Rubenstein 1986).

II. DIRECT EFFECTS

Even a brief perusal of H. G. Andrewartha and L. C. Birch's classic text *The Distribution and Abundance of Animals* (1954) indicates that activity and reproductive patterns of most species are directly affected by climatic conditions. Vertebrates, for example, may huddle for warmth or show shifts in seasonal activity. Direct responses are perhaps most easily seen in ectothermic species, whose reliance on external sources of heat for metabolism makes them sensitive to changes in ambient temperature, while endothermic animals may buffer themselves from climate effects by maintaining constant body temperatures regardless of ambient temperatures. This section examines two types of direct effects: first, changes in insect metabolism, behavior, and resultant geographical ranges, and second, possible changes in reproduction and life histories for a wider range of organisms.

A. Climate as a Determinant of Geographic Range in Insects

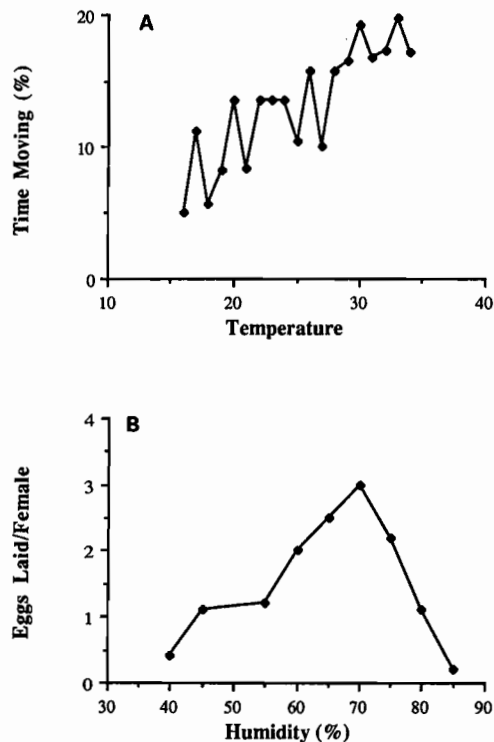
Because the metabolism of insects is directly affected by ambient temperature, climate change can directly affect the population densities and geographic distributions of insects by changing the ambient temperatures within their ranges. An increase in local temperature, for example, can speed up insect metabolism, with resultant effects on local population density. Predicting effects on insects is difficult because insects can buffer the effects of temperature behaviorally—by seeking shelter, for example—and herbivorous insects are also limited by the presence of host plants they need. Nonetheless, it is possible to draw some general conclusions about how climate might change insect distributions by looking at their basic physiological and related behavioral responses to climate variables (see chapter 8 for physiologically derived models of plant distribution).

Insects' metabolic activity and resultant behavior patterns fall into distinct types, depending on how their performance, as measured by traits such as basic metabolism and fecundity, responds to climate variables, no-

tably temperature and humidity. The first type of response is linear, where continued increase in a climate variable, such as temperature, results in continued increase in the biological response. An example is shown in part A of figure 14.1, where locust (*Locusta migratoria*) activity increases linearly as long as temperature increases (until lethality). In general, as activity and feeding rates increase linearly in response to temperature, they will in turn enhance growth and fecundity.

A second type of response occurs when an increase in a climate variable increases the biological response up to a point, but thereafter further increase in the variable decreases the response. In such cases, where optimum performance occurs at moderate temperatures (or humidities), the graph of response is

Figure 14.1. Relationships between climate variables and fitness-related responses by locusts. A. The effects of temperature ($^{\circ}\text{C}$) on movement rates. B. The effects of relative humidity on the average number of eggs individual females lay.

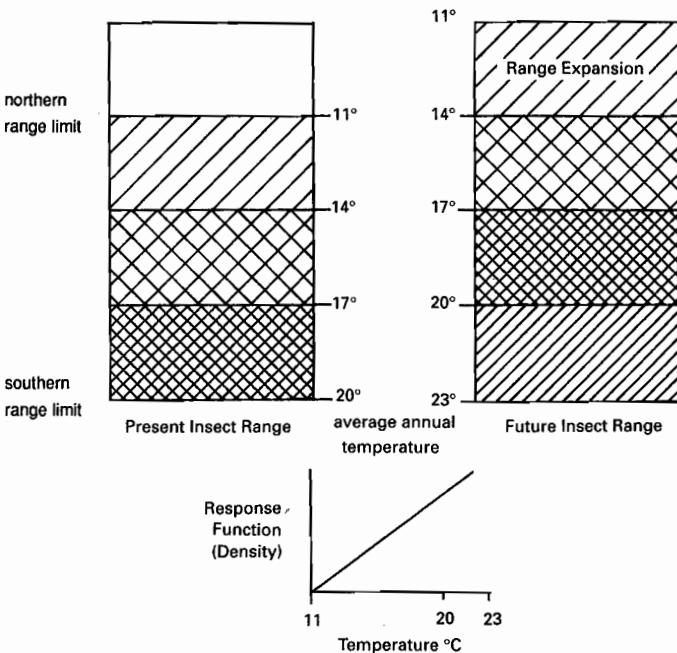


not linear but dome-shaped. In locusts, for example, the rate of egg production is highest only at moderate humidities (fig. 14.1B), dropping off as humidity increases or decreases past the optimum.

Figure 14.2. Range change by a hypothetical insect with a linear response to temperature. Ranges are mapped for two climate states, the present and the future under conditions of global warming with regional temperatures 3°C higher than present values. This model assumes that the insect's response to temperature is dominated by a single trait (for example, basic metabolism or fecundity), whose activity increases with temperature. As the trait increases in value, so does insect population density. On the figure, more cross-hatching indicates greater density. Insects with such linear responses will continue to occupy their present range, at the same time expanding into cooler areas, in this case toward the north. They will have denser populations at the southern end of their ranges than at present. This figure assumes that the southern boundary of the species' range under both present and future conditions is determined not by temperature but by some other constraint, such as a boundary with a superior competitor or the presence of unsuitable soil or vegetation. The northern limit is determined by temperature.

These physiological responses and the behaviors they determine are complex: it is difficult to predict ahead of time how a particular trait will respond to a climatic variable, whether it will show a linear function or one that is domelike. Further, some species may have a linear response pattern for one trait and a nonlinear pattern for another, as typified by the locust.

Understanding these fundamental physiological relationships is important for predicting how insect distributions and ecological relationships would be altered by climate change. Although future distributions would depend on a variety of effects, including insect interactions with vegetation and other animals, we can begin to understand how ranges might change by making the simplifying assumption that ranges of ectothermic species are determined by a single dominant response to a climate variable, a response that is either linear or dome-shaped. Given this assumption, the shape of the response curve will determine the pattern of climate-induced range change. If the dominant response by the hypothetical species to a climate variable is linear, then population den-



sities of the species could rise within its present range. This is because, other factors like competition or predation being constant, a speedup in the life cycle translates into greater production of individuals.

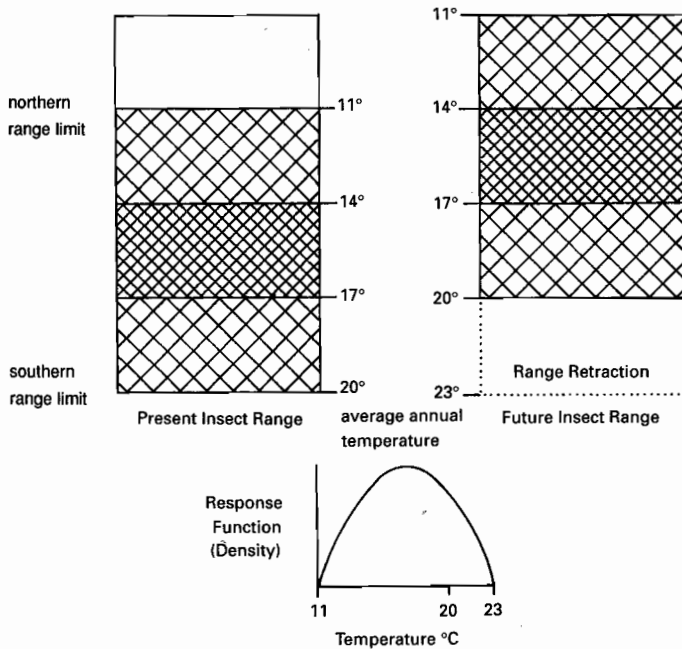
In addition, as shown in figure 14.2, a linear-response species should expand its range into cooler habitat—northward in the northern hemisphere—as habitat there warms enough to be suitable (provided that nonclimatic factors do not restrict expansion), and the species would also maintain its present southern distribution. Insect species with domelike response curves would behave differently. Figure 14.3 shows such a species expanding into warming areas to the north, but

Figure 14.3. Range change for a hypothetical insect with a dome-shaped response to temperature. Climate states are the same as in figure 14.2. Highest density is found at the center of the range, and global warming causes the range to shift toward the north while maintaining its present size. Insect density would remain the same throughout the range, unless affected by factors other than temperature. The model assumes that for this species the northern and southern range limits are both determined by temperature.

its southern boundary also moves northward because the newly raised temperatures in the south exceed physiological limits of the dominant response feature.

Although these scenarios are useful in thinking about a major component of insect response to climate, they make several simplifying assumptions. First, they assume that present-day southern boundaries for linear-response species are determined by nonclimatic factors. This is probably the case for many species, given that at present lethal temperatures are unlikely to be reached at the southern boundary. These scenarios also assume that for species with dome-shaped curves, southern boundaries are now temperature limited, which again is likely but not certain in any particular case.

Second, the outcomes assume that the ranges and densities of the host plants of these insects will respond to climatic changes in exactly the same way as the insects, so that distribution of host plants moves northward and does not limit the insects' temperature-induced range changes. In the real world, there may be changes in plant distribution or



in the timing of critical events, such as flowering and seed set, so that the insect's population growth or range expansion may be limited or possibly even enhanced.

Third, the scenarios assume that individuals of species with dome-shaped response curves will not avoid southern range retractions caused by chronic stressful conditions through the evolution of new behaviors or physiological changes. Obviously, much will depend on the magnitude of the population's genetic variation.

Genetic adaptation could play a role in northward expansion as well, for species with either type of response function. For example, with longer days and warmer climates species that now have a single life cycle per year (univoltine) could evolve the capability for more than one (multivoltine). S. Masaki's (1978) study on crickets suggests how easily proximate control of diapause and nymphal development could be altered to change the number of generations. And with two or more generations of insect pests devouring important crops, the economic impact of such changes could be considerable.

That also has implications for community stability. Because species differ from each other in how key traits respond to climate, and because the functional responses of these traits can determine geographic range, climate change will cause species to move about the landscape independently of each other. This means direct climate effects will be one factor (others include competition and differential dispersal capability) that would cause present insect communities to break up in response to global warming, in a manner analogous to that described by Thompson Webb (chapter 5) and Russell W. Graham for mammals (chapter 6).

Even though we can predict that communities would be disrupted by climate change, it is difficult, given the complexity of dealing with a single species, to project the aggregate response of a community of species. Such a community was investigated in a series of experiments by W. P. McKay and his coworkers

(1986), who varied soil moisture and temperature to assess how these factors influenced the foraging behavior of soil arthropods and their effectiveness in breaking down litter. The arthropods showed increased behavioral activity when, from their point of view, environmental conditions improved, but different groups were favored by different conditions (see chapter 13 for further examples of thermal niche partitioning). Whereas an increase in soil moisture increased termite activity, it decreased the activity of ants. And whereas temperature had no effect on either of these macroarthropods, it did have profound effects on the microarthropods. For both fungivores and predators activity was enhanced by lower soil temperatures. Clearly, what is an environmental constraint for one species may not be for another. And this diversity of responses makes it difficult to assess the long-term ecological consequences, including those that are economically important, of environmentally induced changes in behavior.

B. Reproduction and Life Histories

In addition to changes in activity and ranging patterns, animal reproductive patterns and life histories are also likely to be altered by large-scale changes in climate. For most reptiles an individual's sex is determined by environmental conditions (Bull 1983). In most turtle species only females are produced from eggs incubated at high soil temperatures, whereas in crocodiles and alligators and many lizards the converse occurs (fig. 14.4). Such variations arise because high temperatures during early development accelerate growth and increase final adult size. There is therefore selection pressure for the warmest nests to produce whichever sex achieves the greatest reproductive success by growing rapidly to large size. As long as threshold temperatures for determining male and female development are narrowly and rigidly defined, then large and consistent changes in temperature could cause local extinctions by eliminating one or the other sex from a region. Even if one sex was not eradicated but

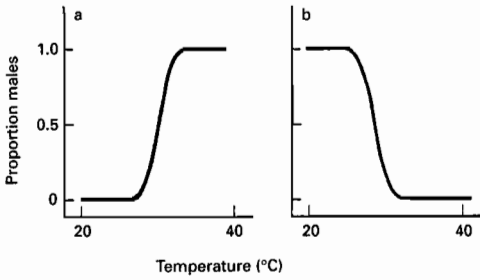


Figure 14.4. Generalized relationships depicting the response of sex ratio to incubation temperature for different types of reptiles. Females develop at low temperatures, as in many lizards and alligators (a). Males develop at low temperatures, as in most turtles (b).

severely limited, the ensuing skewed sex ratios would produce small effective population sizes in the rarer sex, thus limiting a population's genetic diversity. Future potential for adapting to subsequent environmental changes might be so limited that local extinction would occur anyway.

Complete switches in strategies of reproduction might also occur in response to global climatic change. Life-history theory predicts that animals should vary their investment in reproduction depending on their survival prospects relative to those of their young (Horn and Rubenstein 1986). In general, when mortality of juveniles is high but adult mortality is low, it makes little sense for adults to expend much energy producing many small young who are likely to die. Instead, they should produce only a few young at a time, young that often are large or otherwise well endowed to maximize their chance of survival. On the other hand, when juvenile mortality is low, there is an incentive to bear many small young, with a smaller investment in each. Such a life-history variation is exhibited by shad, a fish that grows and matures at sea but returns to rivers to breed and spawn (Gilebe and Leggett 1981). In the southern edge of its range it reproduces copiously, but only once in its lifetime. In the more north-

ern streams of New England and Canada it breeds repeatedly but produces only a few young each time. As theory predicts, massive and exhaustive reproduction occurs in the consistently mild southern streams where juvenile mortality is low, but not in the northern streams where yearly variations in icy conditions make juvenile survival prospects questionable (Shaffer and Elson 1975). Any global environmental change that warmed the northern rivers and made the aquatic environment more consistently benign would switch the northern population from a repeated, or iteroporous, life history to a semelparous one, with a one-shot reproductive effort. The effects that such a shift could have on the structure of entire aquatic communities and the relative abundances of species or the economics of the shad or even the salmon fishery (Gross 1985) could be profound.

The direct effects of global changes in weather need not be limited to temperature and rainfall. Gross changes in patterns of circulation will alter patterns of animal dispersal. Locusts, for example, move from spring to summer breeding grounds and back again with oscillations in the trade winds that are produced by seasonal shifts in the position of the intercontinental convergence (Mikkola 1986). This enables eggs laid during dry periods to hatch after the rains and developing larvae to feast on natural and agricultural greenery. Swarms form and the landscape is devastated. Even though the general patterns of movement are known, it is difficult to predict precisely where locusts will alight and swarms will develop. Changes in global circulation patterns will not only alter where the winds will take such migrants but they could also complicate control measures. In the past, effective, long-lasting, and hence ecologically damaging chemicals could be used to saturate likely feeding areas. Thus adults could be killed whenever they landed in these traps and swarms could be eliminated (Mackenzie 1988). With the shift to safer pesticides that break down more quickly, control can be effected only by spraying the young

and destroying enough of them to prevent the formation of swarms. The imprecise, wide-ranging pest control strategies of the past might have been able to cope with changes in global circulation patterns that either broaden breeding areas or move them to agriculturally richer regions. But any major changes in circulation patterns in conjunction with the new target-sensitive strategies will only make the problem of control more difficult.

III. INDIRECT EFFECTS

Global changes in temperature, rainfall, and atmospheric and oceanic circulation patterns will clearly alter the behavior and life histories of animals. Many changes in behavior, however, occur as indirect responses to previous changes in other components of an ecological community. And although such indirect responses are less easy to detect and make it more difficult to identify cause-and-effect relationships than the direct ones examined above, indirect changes in behavior are common and can have important ecological or evolutionary consequences. For example, the time and activity budgets of animals can be disrupted if the nutrient quality of their forage changes. Ordinarily, if the impala can obtain vegetation composed of 30% water, it does not need to drink and its movements are not restricted to the vicinity of watering sources. In periods of drought, however, the water content of the vegetation drops precipitously, yet the impala's watering requirements remain unchanged. As a result, it must alter its behavior to minimize its chances of incurring water stress. It tends to forage during the coolest times of the day and rest more often in the shade, and if it must forage into the night to maintain its daily ration, it may be forced to feed in open habitats where visibility is greatest (Jarman and Jarman 1973). Clearly, any global change that resulted in the warming and drying of landscapes could lead to massive reorganizations of the time, activity, and movement patterns of animals.

A. Reproduction and Mating Systems

Major adjustments of time and activity budgets often lead to changes in social and reproductive behavior as well. Populations of Alaskan red foxes, after experiencing altered environmental conditions during 1982–84 induced by El Niño–Southern Oscillation in the Bering Sea, exhibited a variety of behavioral shifts (Zabel and Taggart 1989). Before El Niño most of the foxes on an island in the Bering Sea bred polygynously. One male had many mates, as well as a few nonbreeding adult females at the den who helped raise young. As a result, litter sizes and pup survival rates for polygynous parents were equivalent to or higher than those of monogamous ones. After El Niño, however, a major shift occurred in the mating system. Triggered by a reproductive failure of large seabirds, the red foxes shifted their diet to smaller, less abundant, and harder to catch prey. Because this dietary shift led to food shortages, fewer females were able to breed. And those that did, did so monogamously and produced fewer and smaller litters. Changes in behavior in response to environmental changes clearly enabled some animals to make the best of a bad situation. But its effect on the population's ability to maintain itself was large and, in this case, detrimental.

El Niño had dramatic effects on Andean condors as well. In a study that encompassed three populations, M. P. Wallace and S. A. Temple (1988) showed that after the heavy El Niño–induced rains the number of dead and decaying animals increased dramatically along the coast. The population inhabiting this area, unlike the two inhabiting the higher grasslands, normally fails to fledge many young. But after such an influx of resources, it is not surprising that a pulse of reproduction followed. Enough young were produced that the enlarged population provided immigrants to neighboring populations, supplying new genes and linking otherwise isolated populations. As with the red foxes, the ecological and demographic consequences of these global climatic changes may be dramatic.

B. Foraging Behavior

Indirect behavioral and life-history changes are not limited to large, slowly reproducing species, since drought is known to affect many plant processes, which in turn affect insect behavior and reproductive performance (Mattson and Haack 1987). Leaves often turn yellow as chlorophyll production is reduced (Kramer 1983); cavitation, or breaking of water columns, often increases as plants dehydrate (Pena and Grace 1986); and leaf temperatures often rise as stomata remain closed to limit water loss (Mattson and Haack 1987). Each of these changes could make plants significantly more attractive to phytophagous insects, since many are attracted to yellow hues (Prokopy and Owens 1983), have heat or infrared receptors (Altner and Loftus 1985), or can readily detect vibrations (Barr 1969, Carlson and Knight 1969) even in the region of ultrasound (Prosser 1973), which is the type of sound emitted by breaking water columns (Sandford and Grace 1985). Thus drought may increase the likelihood that insects can find suitable food.

And once insects have alighted, other drought-induced changes may even enhance their foraging behavior. Increases in water and heat stress alter the biochemical composition of plants. Typically concentrations of amino acids, nitrates, sugars, and alcohols tend to increase, and many insects have contact chemoreceptors that are sensitive to these compounds. Moreover, they exhibit feeding responses that are proportional to the concentrations of these substances (Städler 1984, Mattson and Haack 1987, Visser 1986). Both the spruce budworm (Albert et al. 1982) and the locust (Mattson and Haack 1987) have peak feeding responses at sucrose concentrations higher than those found in their normal unstressed host plants. In addition, the higher concentrations or a better balance of sugars and amino acids, when coupled to higher leaf or ambient temperatures, may make drought-stressed plants more suitable for the growth and reproductive success of such insects as butterflies, moths, and grasshoppers (Mattson and Haack 1987). For

other sapsucking arthropods, however, increased sap viscosity often lowers feeding ability (Auclair 1963). There is even some evidence that the altered chemical composition of plants enhances the ability of insects to detoxify some compounds (Wargo 1981). High temperatures and low humidities will also limit the ability of pathogens to control populations of phytophagous insects (Wilson 1974, and chapter 16).

Thus drought may indirectly alter the feeding behavior and reproductive performance of insects by increasing water and temperature stress on plants. Compromised defenses and increased attractiveness leave plants susceptible to many types of insects, but usually only for a short time. Normally, as climate improves so does the state of the affected plants, and populations of insect pests ordinarily decline. Of course the return to normal insect levels may be delayed because even normal plants may remain overwhelmed for some time by the outbreak. But if global climate change is not episodic, then the natural plant responses to stress may lead to massive insect outbreaks and chronically large populations that persist until plant abundances decline.

Climate change will not only change the appearance and nutrient balance of individual plants, but it will also change the quality, density, and composition of entire plant communities. For organisms higher up in the food chain, the consequences are likely to be profound. S. Riechert (1986) has shown that the aggressive tendencies of spiders vary dramatically with habitat. In riparian areas where shade keeps the habitat cool, 90% of the ground is available for web sites. Insect prey is abundant, and competition for resources or costs associated with defense of territories is minimal. Moreover, there is no correlation between web-site quality and reproductive success. It appears that most spiders can make a living fairly peacefully and are performing about equally well. In open grassland areas, however, temperatures are extremely high and winds exert a significant drying effect. Only about 12% of the substrate is suit-

able for web sites and insect abundances are low. Aggressive competition is severe, and a strong correlation exists between web-site quality and reproductive output. The simplest game-theory models predict that the probability of severe aggression should increase as the value attached to securing a resource increases or as the costs of fighting, either in terms of energy expended or damage incurred, decrease. Since in the grassland habitat the opportunity costs of not having a web site are greater than those in the riparian habitat, it is not surprising that aggression is much more frequent and intense in the grasslands (table 14.1). Whereas contests in riparian habitats are likely to escalate to display, those in grassland areas often proceed beyond display to threat. Thus, if the effect of global climate change is to make critical resources scarce, not only should levels of specific aggressive behaviors increase, but also should the nature of individual social interactions become qualitatively different.

C. Social Behavior

On a larger scale, climate changes that affect vegetation quality often lead to changes in the patchiness of habitats and large-scale alterations of the landscape. Altering the number, size, and juxtaposition of habitats has profound effects on the social systems of a variety of large-bodied and wide-ranging species such as ungulates, and these in turn influ-

ence the genetic structure and recruitment abilities of populations. In elephants, for example, group sizes and composition change seasonally in response to seasonal differences in vegetation abundance (Western and Lindsay 1984). After the rains, when grasses begin growing rapidly, elephants graze on the plains. Because the grasslands stretch more or less continuously for hundreds of kilometers, little competition occurs when feeding. As a result, elephant females aggregate in large herds. With the flush of quality vegetation many come into estrus and become reproductively active. Typically, males remain sexually active for a short period of the year and advertise their condition, termed musth, with a variety of secretions (Poole and Moss 1981, Poole 1989a). Only the most dominant males come into musth immediately after the rains. Because the reproductive value of gaining access to the female groups is so high, the formation of massive female aggregations effectively incites male-male competition, with only the most capable being able to attach themselves to these large groups and being able to aggressively drive away interlopers. In the dry season, however, after the grasses on the plains cease growing and become cropped so that there is too little biomass to support such large-bodied ungulates as elephants, the elephants retreat to the swamps, where other grasses and browsable leaves remain. The patchy and closed nature of these

Table 14.1. Comparison of agelenopsid spider contests between opponents from sites of varying quality. Opponents were equal in weight, within 10%. Adapted from Riechert 1986.

Site quality	Cost	Length		Outcome
	Estimated energy expended	Number of acts	Number of bouts	Probability that owner will win
Grassland				
Poor: Surface	123.3	11.9	1.9	0.56
Average: holes	344.0	31.4	3.0	0.76
Excellent: holes	556.7	51.6	3.7	0.92
Riparian				
Excellent: rocks	126.2	13.5	1.8	0.92
Excellent: grasses	146.2	14.5	2.1	0.60
Excellent: leaf litter	185.5	16.1	2.1	0.89

habitats forces the large elephant herds to fragment into smaller family units. In addition, declining vegetation abundance and quality reduce the number of females that remain reproductively active. With fewer reproductive opportunities, dominant males go out of musth at this time of year while subordinate males enter it (Poole 1989a).

The consequences of these seasonal shifts are many. First, more females are sexually receptive after the rains, and they are also more localized than in the dry season. And second, given these seasonal differences in the distribution and abundance of sexually active females, dominant males have greater access to, and control over, reproductive females than do subordinate males. As a result, the reproductive success and Darwinian fitness of dominants are likely to exceed those of subordinates (Poole 1989b). Thus any global change in climate that would either affect the timing or duration of the rainy season could have profound effect on the genetic structure of elephant populations, as long as dominance is not strictly an age-related phenomenon. If, for instance, dry-season conditions came to predominate, elephants would be spending more time in smaller and fragmented groups. The ability of one or a few dominant males to control matings and sire a disproportionate share of the offspring would then be limited. More subordinates would be able to mate and a more equitable distribution of genotypes would be disseminated among the young. The effect of such a dramatic shift in the genetic structure of the population is hard to ascertain, but the change itself will be very real.

Similar social changes occur in many other ungulates. Topi, for example, exhibit lek mating systems, in which males defend small territories where females come to mate in a landscape characterized by sharp gradations in relief (Gosling 1986). In such habitats males can control elevated open sites where predation is unlikely because of excellent visibility, and females can feed free of male interference in the more productive intervening valleys. In areas of rolling grasslands where relief

is more shallow and habitat differentiation is less distinct, small groups of females are instead defended by single males. Thus if global climate change alters the patterning of the landscape, it is likely that mating and social systems of animals living off that landscape will change.

Social organization can directly affect the reproductive success of a population. Horses live in a variety of societies (Rubenstein 1981, Berger 1986), and this variability illustrates how the social relations of different populations affect population dynamics. Despite significant ecological and social differences, all horse societies can be characterized by one general rule: unrelated females initiate associations with males and live in so-called harem groups whenever topography permits (Rubenstein 1986). The males they prefer are generally the most dominant, because only such males limit harassment from other males seeking sexual access. And protection increases the likelihood that females will rear offspring to the age of independence (Rubenstein 1986).

The following example shows not only the effect of social structure on reproductive success but also that social structure itself can be determined by the patterning of resources. On a barrier island off the North Carolina coast before 1980 one population of horses lived in traditional harem groups, whereas another did not. The population with harems ranged over an area of ten square kilometers where grazing swards were continuously distributed. The other lived in an area where tall dunes and dense maritime forest fragmented grassy areas into patches of variable size. In the largest patches large groups could form, but in the small ones intense competition for food caused groups to fragment. Thus a fission-fusion society developed and made it impossible for males to associate permanently with any group of females. Males wandered solitarily, and aggressive contests occurred whenever two or more males encountered reproductive females. Since the contests occurred near the females, harassment of females was high and their ability to

forage was reduced. When the per capita reproductive successes of females from the different populations were compared, those in the harem society were higher than those in the fission-fusion society despite the increased vegetation available to females living in the latter. Thus before 1980 it was not surprising that the number of horses in the fission-fusion population remained unchanged, while the number in the harem population kept increasing.

After 1980 the social organization of the population in the patchy grasses changed. Dredging of the channel separating the island from the mainland increased the area of the island in the vicinity of the fission-fusion population. Because the new land was flat, the grasses that soon covered it were distributed continuously. Within two years harems developed there, harassment of females declined, per capita reproductive success improved, and the population began to increase in size. Again, a change in landscape altered a population's social organization. But even more important, the social change led to a significant change in the population's dynamics and its ability to expand.

This type of indirect effect can not only alter the shape of an animal's society, but it can also influence the composition of animal communities or even humankind's conservation efforts and ability to manage endangered species. If rare species find themselves in or are reintroduced into altered habitats, the societies they develop may make it impossible for them to maintain themselves. Such outcomes would complicate conservation efforts.

IV. CONCLUSIONS

These examples illustrate that global climate change is likely to alter the behavior and life histories of many types of animals. Whether these effects are the direct or indirect result of changes in temperature, moisture, or circulation patterns, the consequences for the genetic structure and demographic properties of populations are likely to be dramatic. The examples and the changes they illustrate re-

fect natural responses to existing levels of environmental variability or change. There is no reason to suspect that these variations are any more drastic than those envisioned for future global changes in climate. In fact, they might underestimate the changes animals are likely to experience. They certainly are more analogous to anticipated changes in average tendencies than to changes in the extremes.

Actual studies that specifically examine the expected effects of global climate changes due to the greenhouse effect are rare. It is hoped that the speculative accounts and hypothetical predictions can be tested by direct experimentation. By perturbing ecological microcosms, behavioral changes and their ecological impact can be monitored. But more important, biologists need more finely tuned predictions from the climatologists as to what conditions animals at a local level are likely to experience. This is especially important for forecasting indirect effects, since small differences in vegetation or landscape can produce markedly different alternative behavioral outcomes.

At the same time, however, ecologists must begin identifying a few key ecological habitats worthy of detailed ecological study. Important species, those that carry out key functions in different locales, must be studied so that the strength and direction of indirect effects on behavior and life history can be evaluated. By identifying these patterns as well as the major variables, global modelers will gain insights into what variables will make their climate predictions more useful.

V. SUMMARY

Changes in climate will profoundly affect the behavior and life histories of animals. Increases in temperature and changes in humidity will often be direct. For many insects, as temperature and humidity increase, developmental rates, speed and distance of movement, and fecundity will generally be enhanced, and these changes should have pronounced effects on many ecological processes. For the many reptiles whose sex is environmentally determined, slight changes

in temperature will alter the relative proportion of sexes in a particular locale and thus could potentially disrupt population dynamics. Moreover, global changes in wind circulation will affect the migratory routes of many insects, such as locusts, and any change that alters the balance between adult and juvenile mortality will also change a species' life history, sometimes as dramatically as changing it from a repeated to a one-time breeder.

Other effects will be indirect, since changes in climate will change features of the landscape and they in turn will alter the behavior of the animals residing in those habitats. At the moment, however, the exact ecological consequences of these changes are difficult to predict; the magnitude of the temporal and spatial variation associated with anticipated climatic change is unknown, and even small variations could eventually cause major swings in behavioral outcomes. Nevertheless, some trends can be perceived. For example, changes in global circulation systems often disrupt the population dynamics of predator species because critical features of the biology of their prey are disrupted. Moreover, wholesale stressing of plant communities often enhances the foraging ability of herbivorous insects, which in some instances will reinforce the stresses already being experienced by the plants. Major changes in the landscape, including shifting of biome boundaries, will also occur and lead to changes in the social behavior of a variety of animals. Whereas increases in aridity tend to heighten the intensity of aggression displayed by such species as spiders, the same types of landscape change will lead to major adjustments in the daily cycle, time budgets, and mating systems of such large-bodied species as grazing ungulates. The long-term consequences of these behavioral changes on the genetic structure or demographic dynamics of populations are likely to be great.

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