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ON APPLYING BEHAVIORAL MODEL SYSTEMS TO LANDSCAPE ECOLOGY.

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The impact of habitat loss and fragmentation of remaining habitats on the distribution,

persistence, and metapopulation dynamics of plants and animals is a major concern in

conservation biology and landscape ecology (Harris 1984; Wiens et al. 1993; Lidicker 1995;

Hanski and Gilpin 1997). Much of our understanding of how habitat loss and fragmentation

affect native populations is through retrospection, speculation, or modeling rather than direct

quantification or experimentation. Evidence of whether or not experiments and observational

studies corroborate or substantiate predictions of mathematical models is equivocal (Lamberson

et al. 1994; Schumaker 1996). One of the reasons for this discrepancy is that species within a

taxon often are treated as mathematical entities (i.e. all individuals are "average") and

individual-, sex-, and species-specific differences in response to fragmentation are not taken into

account (Andrén 1994; Lima and Zollner 1996). Some of the differences in species responses to

fragmentation can be explained by differences in their behavioral systems, dispersal ability, life

history, trophic level, sociality, and overall responses to changes in habitat size, connectivity, and type of matrix.

In that experimental studies, or even observational studies are not possible on endangered, large, or rare species, ecological model species or systems (EMS) are sometimes used to test predictions of how a species will respond to some perturbation (Ims and Stenseth 1989; Wiens et al. 1993; Ims et al. 1993; Wolff et al. 1997). Several studies have used small mammals in enclosed or manipulated habitats as EMS's to evaluate responses to loss and fragmentation of habitat (e.g. Ims et al. 1993; Barrett et al. 1995; Diffendorfer et al. 1995) and the theoretical application of mammalian responses to landscape ecology have been discussed in Lidicker (1995). The results from these studies are then applied to other species or situations to predict similar responses (e.g. comparing territoriality of voles with that of capercaillie grouse (*Tetrao urogallus*, Ims et al. 1993). EMS's may have their utility, but whether movements of voles in enclosures represent movements of cougars in southern California (Beier 1995) or spotted owls (*Strix occidentalis*) in western Washington (Lamberson et al. 1994) is doubtful (scientific names not presented in the text are listed in Appendix 1). I propose that species may not necessarily be good surrogates for other species per se, but rather behavioral systems might be more appropriate for making comparisons and predictions among species. Certain aspects of behavior, such as territoriality, sex-biased dispersal, and sociality might be more similar across species, than are other traits such as phylogenetic relations, body size, or other aspects of ecology. An understanding of the behavioral ecology of species should provide further insight into how species respond to fragmented landscapes. In conjunction with behavior, I describe

how life and evolutionary history and degree of habitat specialization can affect a species response to fragmented landscapes.

Colonization of Habitat

Evolutionary History

The rate and(or) probability of a species colonizing distant patches may be in part, a function of its evolutionary history. If a species evolved in stable continuous habitat it may respond very differently to fragmented habitats than a species that evolved in a patchy or frequently disturbed environment (Merriam 1995; Lima and Zollner 1996). In western North America, elk are frequently associated with mature forests or edge habitat, whereas they apparently spent much of their evolutionary history in North America as an open steppe habitat species (Guthrie 1968, Geist 1971). Black bears of eastern United States are primarily forest-dwelling, whereas in western and northern North America they are frequently associated with partially open habitats (Powell 1997). Weddell (1991) argued that Columbian ground squirrels never evolved dispersal strategies suited to colonization of isolated pockets of habitat because steppe vegetation is stable relative to the lifetime of a ground squirrel. Black-tailed prairie dogs likewise do not migrate to unoccupied natural patches (Garrett and Franklin 1988). On the other hand, alpine marmots, which occupy isolated rock outcrops interspersed in alpine mountains appear to be adapted to dispersal and colonization of this patchy resource (Van Vuren 1994; 1997). White-footed mice (*Peromyscus leucopus*) also readily colonize isolated woodlots and persist as a metapopulation (Middleton and Merriam 1981). Wolves often follow prey such as caribou (*Rangifer tarandus*) or deer (Weaver et al. 1996) and lynx disperse over large distances in search of food during

3

snowshoe hare declines (Murray et al. 1994). Snowshoe hares, moose, and grassland voles

which exploit early successional or frequently disturbed habitats should also be good colonizers

(Wolff 1980; Hik 1995). Species such as pronghorns (*Antilocapra americana*) and jack rabbits

that have evolved in open plains habitats and avoid forested areas, probably would not be good

colonists if they had to disperse through barriers of wooded habitats. Thus, various aspects of the

evolutionary history of a species may influence its tendency to move across a habitat mosaic.

Habitat Mosaics: Generalists vs Specialists

Most population viability models are based on habitat preferences or a habitat suitability index

(HSI) for the species (Morrison et al. 1992). Unfortunately, most species do not visualize or

utilize habitat based on its description on an aerial photo or landsat image. Rather, many species

have habitat requirements that include a mosaic of habitats, each component being necessary but

not sufficient for successful colonization. For instance, bats typically require a covered roosting

site, often with a narrow access passageway such as caves, tree hollows, or manmade dwellings

(Bradbury 1977). Preferred and suitable foraging areas are not necessarily coincident with

roosting areas. Bats may feed on nectar, fruit, blood, fish, or flying insects, all of which may or

may not be in the immediate vicinity. Opossums and raccoons require hollow trees for nesting,

but frequently forage in open habitats, along streams, or in urban settings. Bears may shift home

range use from mature forest or grazing areas in spring to spawning salmon streams during

summer, and berry patches in fall (Powell 1997; and others), all of which may fall into different

vegetation classifications. Marten typically spend 95% of their time in forest habitats but forage

extensively for voles in adjacent grassland habitats (Zielinski 1982). Male and female ungulates

4

typically segregate and use different habitats for much of the year (Main et al. 1996; Bleich et al. 1997). Sexual segregation into different microhabitats also was recorded for cotton rats (Lidicker et al. 1992). Therefore, specific habitat requirements that include all the requisites for life must be considered for species that have different feeding and nesting areas, seasonally available resources, and sex-specific requirements.

In contrast, some species which are habitat specialists avoid mosaics and perceive them as a barrier to dispersal. In a comparison of colonization ability of North American and European rodents, Liro and Szacki (1995) concluded that bank voles and chipmunks (*Tamias striatus*) were forest habitat specialists and would not be good colonists in fragmented habitats whereas yellow-neck mice (*Apodemus flavicollis*) and deer mice, habitats generalists, would readily cross habitat mosaics and be good colonists. North American red-backed voles (*Clethrionomys* spp.) and *Peromyscus* would be similar to European *Clethrionomys* and *Apodemus* species (see also Wegner and Henein 1991). Marten (*Martes* spp) also are forest specialists and seldom travel greater than 25 m into open habitat (Bissonette and Broekhuizen 1995) which probably restricts their ability to colonize new patches interdispersed among an open habitat matrix. Laurance (1995) concluded that arboreality also might decrease a species chances of colonizing patchy habitats. In a study of the distribution of mammal species in an Australian landscape, Laurance found that populations of terrestrial generalists were more stable and evenly distributed across a landscape whereas arboreal marsupials were more apt to go extinct or be absent from forested habitat fragments. North American tree squirrels should respond similarly. Forest-dwelling spotted skunks should have a more difficult time dispersing across open fields than would striped skunks which are adapted to fragmented landscapes.

5

Similarly raccoons and opossums which are adapted to urbanization should be able to cross human-occupied areas more readily than would wolverines and fishers which tend to avoid human contact.

Species that live on habitat islands such as hyraxes (*Procavia johnstoni* and *Heterophyrax brucei*) which occupy rock outcrops in Africa (Hoeck 1982), muskrats which are confined to ponds (Messier et al. 1990), and pikas which occupy isolated talus slopes (Smith and Ivins 1983) are apparently reluctant to leave their island habitats. Thus, species that evolved within and even may require a mosaic of habitats should be better colonists than habitat specialists that have evolved within a given habitat type and are probably reluctant to cross habitat matrices.

Spacing Behavior - Female Territoriality

Perhaps one of the most influential factors that determine how a species responds to changes in habitat area is territoriality. Territoriality is defense of an area such that it becomes relatively exclusive with respect to rivals (Maher and Lott 1995). In that successful colonization of a patch requires immigration and establishment of females, I limit my discussion to situations in which females actively defend territories against other females to provide exclusive access to breeding space (Wolff 1997).

Population viability models rely extensively on females occupying exclusive space such that only one breeding effort takes place on a given home range area at a time (e.g. Lamberson et al. 1994; Schumaker 1996). For many species of mammals this is appropriate; for others it is not (Wolff 1997). Female territoriality occurs in species that have nonmobile altricial young that are

6

deposited in a den or protected nest site. Mammal species with precocial young and(or) altricial young that are carried with the mother (such as marsupials and primates) are not territorial (Wolff 1997). Therefore, female territoriality commonly occurs among the insectivores, rodents (squirrels, mice, and voles), rabbits, carnivores, and prosimian primates, and does not occur among the ungulates, hystricognath rodents, hares, marsupials, and most anthropoid primates. In territorial species such as red squirrels, tarsiers, wolves, and rabbits, females require an individual territory to breed (see exceptions below), whereas in nonterritorial species, exclusive space is not a requisite for reproduction (Wolff 1997). For instance, in ungulates such as bighorn sheep, elk, or bison (*Bison bison*), all females have the opportunity to breed irrespective of space. Social pressures do not prevent any female from breeding in nonterritorial species. The important point here, is that in territorial species, the size of breeding population is limited by the number of breeding sites (territories) available in a habitat (Wolff 1997). This same relationship does not hold for nonterritorial species.

Some exceptions to the one-female-one-breeding-effort/territory rule occur. The social structure of most mammal species is that young males disperse from the social unit and daughters are philopatric and remain in or near their natal site (Greenwood 1980; Pusey 1987; Brandt 1992; Wolff 1993 and see Dispersal section below). Female philopatry often results in the formation of kin groups or female alliances that share the same space such that if space is limited, daughters can breed on their mother's territories. This pattern of shared space commonly occurs among prairie dogs (Hoogland 1995), marmots (Armitage 1981) and many species of mice and voles (Jannett 1978; Wolff 1985, 1994; McGuire and Getz 1991; Lambin 1994; Salvioni and Lidicker 1995). In contrast, only one female breeds on a territory in red foxes (Allen and Sargeant 1993),

7

wolves (Mech 1970), dwarf mongooses *(Helogale parvula*; Creel et al. 1992) red squirrels (Price and Boutin 1993), and common marmosets *(Callithrix jacchus*; Digby 1995). Thus, an understanding of the social relationships among related females and their tolerance of shared breeding space will allow more accurate predictions of the reproductive potential for a given area of habitat.

Sociality and Conspecific Attraction

Smith and Peacock (1990) already have demonstrated that conspecific attraction can affect metapopulation colonization rates. Weddell (1991) reported that in ground squirrels colonization of new habitats did not occur because emigrants settled near other squirrels rather than in vacant patches. Similar results were found for prairie dogs (Garrett and Franklin 1988). New coteries or populations of prairie dogs and ground squirrels are formed by fusion or fission of established colonies (Michener 1983; Halpin 1987) and not by colonization of individuals into vacant patches. In contrast, the tendency to disperse and colonize distant patches should be less affected by conspecifics in asocial species, or those that are not attracted to conspecifics per se, such as hares, mink, opossums, and moose.

Patch Occupancy and Optimal Group Size

Another factor that determines the number of individuals in a habitat patch is that which affects optimal group size. Optimal group size in turn is dependent on several ecological and social factors. Optimal group size in African hunting dogs is based on hunting energetics (Creel and Creel 1995) whereas in lions, group size apparently is not based on predator efficiency, but rather

8

on the success of the pride in protecting cubs against infanticide or in defense of carcasses (Packer et al. 1990). Optimal group size in this case is dependent on the size of other groups in the area. Optimal group size in ungulates such as bighorn sheep, pronghorn, and bison may be based on predator vigilance such that a minimum group size is a necessary trade-off between time spent in vigilance and eating (Berger 1978; Belovsky 1986). A minimum group size is apparently also required for colonial or communal species such as prairie dogs and ground squirrels such that colonies do not exist below a minimum threshold number regardless of patch size (Weddell 1991; Hoogland 1995).

Source-sink Habitats and Reproduction

Just because members of a given species are found in a given habitat, does not mean that the habitat is optimal or even adequate for the species. Animals will often occur in suboptimal or sink habitat (Pulliam 1988), but may not necessarily reproduce there. Weddell (1991) found that some dispersing subordinant male Columbian ground squirrels temporarily settled in unoccupied habitat, but were not successful colonists. J. Wolff (unpubl.) found a small group of "bachelor" taiga voles in suboptimal habitat; there were no females in the habitat and the males were not breeding. Robinson et al. (1992) and Diffendorfer et al. (1995) similarly found that small rodents were occupying small grassland patches, but successful breeding occurred only in larger patches. Typically in ungulates, dominant males occupy the best habitats and groups of subordinant bachelor males are relegated to suboptimal habitats (Jarman 1974, Gosling 1986). Thus, the suitability for reproduction of a given habitat must be taken into consideration when concluding if occupation is synonymous with successful "colonization".

Dispersal

Barriers and Colonization

An important component of mammalian behavioral systems is dispersal (Stenseth and Lidicker

1992). From an ecological perspective, dispersal has demographic consequences for a population

in that it can stabilize densities and provide gene flow and genetic panmixia. From a behavioral

perspective, dispersal separates opposite-sex relatives and reduces the chances of inbreeding

(Pusey 1987; Brandt 1992; Wolff 1993, 1994). On the other hand, delayed dispersal can result in

delayed sexual maturation (e.g. Creel and Creel 1991; Wolff 1992, 1997 and references cited

therein), cooperative breeding (Powell and Fried 1994; Solomon and French 1997), or possible

inbreeding (Smith and Ivins 1983). In large continuous populations, animals are free to move

throughout the habitat without consideration of ecological or physical barriers. However, in

fragmented landscapes, dispersal can be deterred or prevented depending on the type of barrier

and presence and absence of corridors (Fahrig and Merriam 1985).

Ecological Barriers

What constitutes a barrier will vary depending on the mobility, natural history, and habitat

specialization of a species. Small fossorial mammals such as shrews, moles, and gophers should

have a difficult time crossing interstate highways, rivers, and even small streams whereas more

mobile and terrestrial species such as bats and larger mammals can cross such barriers with ease.

On the other hand, aquatic habitats provide an avenue for dispersal for species such as water

shrews (e.g. *Sorex palustris*), otters, beavers, and nutria (*Myocastor coypu*), whereas terrestrial

habitats are a barrier to movement of these species. A 15-m strip of mowed grass was a partial

barrier to movement for tundra voles (*Microtus oeconomus*, Andreassen et al. 1996a) and a 4-m strip of barren ground was a barrier to movement in gray-tailed voles (*Microtus canicaudus*, Wolff et al. 1997); whereas deer mice readily cross open areas greater than 12-m wide (J. Wolff unpubl) and white-footed mice cross open fields >1 km (S. Vessey pers. comm.). *Microtus* voles in general have evolved in grasslands which provide considerable cover, whereas *Peromyscus* are more open-habitat generalist species (Baker 1968); therefore what is a barrier to a *Microtus*, may not be a barrier to a *Peromyscus*.

Behavioral Barriers - Corridors

The negative effects of fragmentation on populations can be reduced by connecting isolated fragments by narrow strips of habitat referred to as movement corridors (Harris 1984; Bennett 1990, Simberloff et al. 1992). Empirical evidence for if and(or) how animals use corridors, however, is minimal (Hobbs 1992; Simberloff et al. 1992; LaPolla and Barrett 1993; Andreassen et al. 1996b; Davis-born 1997) and may not fit the assumption that bigger is better (Noss 1987; Harrison 1992). For instance, optimal width of corridors for meadow voles (LaPolla and Barrett 1993) and tundra voles (Andreassen et al. 1996b) was 1 m. Voles were reluctant to enter narrower corridors while linear movement in wider corridors was hampered by cross-directional movements. Wider corridors may be perceived as habitat rather than an avenue for directional movement and become permanently occupied. Occupancy of corridors should affect territorial and nonterritorial species differently. For instance, if an individual establishes a territory that encompasses the width of the corridor, other individuals will be less able to move along the

11

corridor to adjacent patches than if the corridor were not occupied. For nonterritorial species movement should not be deterred along such stretches of habitats.

Dispersal Distance

Dispersal is a component of vertebrate behavioral systems that contributes substantially to colonization of vacant habitats and fragmented landscapes. Estimates of the tendency to disperse and dispersal distance are used to predict the likelihood of a given species colonizing a vacant habitat or crossing a fragmented landscape. Estimates of dispersal patterns and distances are also used in spatially explicit population viability models (e.g. Lamberson et al. 1994; Schumaker 1996). Dispersal patterns vary considerably among species primarily with respect to dispersal distances, which sex disperses, and the tendency to disperse in the first place. However, various aspects of a species life and natural history and behavioral system can affect dispersal patterns among mammals (Koenig et al. 1996). I expand on the paper by Van Vuren (1997) in which body mass of 33 mammals was used to estimate median dispersal distances for all mammals. I used data on maximum dispersal distances for species of mammals and discuss the implications of dispersal distance and various aspects of a species social system and life history that contribute to dispersal patterns and the propensity for a species to colonize new habitats.

I obtained dispersal distances for as many species as I could find from the original literature. However, dispersal distances are rarely studied directly for mammals, so data on dispersal distances often are obtained from basic studies on animal demography or from data that were obtained inadvertently in radio-telemetry or mark-recapture studies. Much of the data on dispersal distances are anecdotes and often represent record distances or in some cases minimal

12

distances based on the size of the study or census area (see Koenig et al. 1996 for discussion on

data limitations). Though dispersal distances vary considerably by sex, species, age, and habitat,

and sample sizes are always small, I obtained as much reliable data as I could find, and then

regressed log mean maximum dispersal distance against log body mass to estimate dispersal

distances for other species. Many mammalian life history traits scale allometrically to body mass

(e.g. Peters 1983; Calder 1984) including home ranges sizes (McNab 1963; Harestad and Bunnell

1979; Holling 1992). I used a least squares linear regression of $\log_{10}$ of "mean maximum

dispersal distances" against $\log_{10}$ of body mass for 59 species of mammals for which data were

available. The mean maximum dispersal distance was an estimate of the distance within which

most (usually >90%) of the animals were caught. For many species, I found data for only a few

individuals and used these values if they seemed reasonable. I used data primarily on dispersal of

juveniles from the natal site and only adult dispersal data when those of juveniles were not

available. I did not use dispersal data from translocated animals or record dispersal distances.

For some species such as mountain goats, bighorn sheep, and sea otters, I had only total lifetime

movements of animals and used these distances. Body masses for mammals were obtained from

Eisenberg (1981), Chapman and Feldhammer (1982), and Silva and Downing (1995) and if

available I used the same masses as Van Vuren (1997).

The dispersal data are in Appendix I and the allometric relationships between dispersal

distance and body mass are listed in Table 1 and shown graphically in Figs. 1 and 2. The

allometric relationships for dispersal distance as a function of body mass for all mammals gives

an r^2 of .868. Carnivores have a steeper slope than do herbivores and omnivores. The slopes are

relatively similar for males and females, however females have a lower intercept than do males

(Fig. 2). In general, males disperse farther than do females and carnivores farther than do herbivores or omnivores. Some of the species that show the shortest dispersal distances and fall below the regression lines in Fig. 1 are those that are highly social such as the ground squirrels or those that are confined to very patchy habitats such as pikas and pond-dwelling muskrats. Those mammals that are the farthest below the regression line in Fig. 1 are all females and include the field and meadow voles, wambenger, pika, muskrat, and gray fox. Although these equations predict dispersal distances for all mammals, deviations from this expected dispersal distance are expected to occur for the reasons discussed above and below.

Which Sex Disperses

In most mammal species, females are relatively philopatric often remaining in or near their natal site and dispersal is male-biased (Greenwood 1980, Pusey 1987, Wolff 1993). Thus, the probability of colonizing and establishing a breeding population in new sites or distant patches is often less than would be predicted based on an estimated dispersal distance for the species. Even though both males and females are listed as dispersing in Appendix 1, males usually disperse farther and at a much higher frequency than do females in all species except the kangaroo rats, red squirrels, snowshoe hares, mountain hares, beaver, porcupines, wombats, European badgers, arctic and red foxes, lynx, coyotes, dingoes, wolves, and opossums. Females do occasionally disperse in the other species, but in general, females of these species remain relatively close to their natal home range and often form female kin groups (Greenwood 1980, Holekamp 1984; Kevles 1986, Boonstra et al 1987, Wolff 1994, 1995, 1997). Among large carnivores, female grizzly bears remain near their natal site and are not likely to colonize new habitat; whereas

female wolves, lynx, and cougars frequently move long distances (Weaver et al. 1996). General characteristics of species in which both sexes disperse at comparable rates and distances include a monogamous mating system (such as exhibited by many species of canids), species in which both sexes individually defend burrow systems and food caches (such as kangaroo rats and red squirrels), or species that are not territorial (such as hares, porcupines, and opossums; summarized in Wolff 1997).

Factors Contributing to Variance in Dispersal Distances

Density, Territoriality, and Dispersal

The rate of dispersal of individuals away from their natal site is, in part, a function of the species behavioral system. Territoriality can impede movement of animals if all the suitable space is occupied and individuals are thus not able to cross undefended space. This type of barrier to movement is referred to as a social fence (Hestbeck 1982) and results in an inverse density-dependent dispersal pattern in territorial species (Wolff 1997). In contrast, in nonterritorial species in which habitat is not actively defended, individuals can move without social impediment at any density. Thus in nonterritorial species, emigration should be density-independent (Wolff 1997). A decrease in emigration rate has been reported for high densities of several species of territorial mammals (e.g. montane voles, *Microtus montanus*, Jannett 1978; white-footed mice; Wolff 1992; prairie voles, *M. ochrogaster*; Maguire and Getz 1991). On the other hand, emigration should not be delayed in species such as deer, elk, porcupines, opossums, and other species that do not defend territories.

Delayed Emigration

Any type of barrier, whether it be ecological, physical, or behavioral can result in delayed

emigration and its demographic consequences (e.g. frustrated dispersal, Lidicker 1975). A

common consequence of delayed emigration is delayed body growth and reproductive

suppression of young females as long as they remain in their family group or in the presence of

other adults. The proximate mechanisms for reproductive suppression may be to reduce

competition within the natal site (Abbott 1984; Digby 1995), to prevent inbreeding with close

relatives (Wolff 1992; 1997), or in response to the threat of infanticide from adult females

(Wasser and Barash 1983; Abbott 1984 ; Digby 1995; Wolff 1997). Delayed emigration can also

lead to cooperative breeding (Powell and Fried 1994; Creel and Waser 1994; Solomon and

French 1997). In all of these situations, reproductive suppression is a response to immediate

behavioral situations that are created because normal dispersal patterns are prevented.

Behavioral reproductive suppression does not appear to occur in nonterritorial species. Thus, the

behavioral and demographic responses to delayed dispersal should be a function of the species

behavioral system.

Delayed Emigration and Longevity

What does lifespan have to do with the demographic consequences of delayed emigration and

delayed reproduction? The probability of extinction, colonization, and persistence of a species in

a fragmented landscape is a function of life expectancy. In general, in long-lived species with

high annual survival rates, delayed sexual maturation and(or) foregoing a reproductive event has

relatively little long-term consequences compared to a species with a short life expectancy. For

instance, whether a bear, wolf, or elk breeds as a 3-year old or reproduction is delayed until the

age of 5 or even 6, should have less consequences than if a vole or mouse delays sexual

maturation for even 3- to 4 weeks. The reproductive lifespan for most voles is 3-5 months with

2-week survival rates typically around 0.8 (Taitt and Krebs 1985; Schauber et al. 1997) compared

to >10 years longevity and 0.9 annual survival rates for larger mammals (Read and Harvey 1989;

Promislow et al. 1991). In Belding's and golden-mantled ground squirrels (*S. beldingi* and *S.*

lateralis), (which may live for up to 9 years) reproduction may be curtailed in years of

unfavorable weather with little long-term demographic consequences (Morton and Sherman

1978; Phillips 1984; Smith and Johnson 1985). If ecological or behavioral conditions are

temporarily unfavorable for reproduction in a short-lived species, a population can go extinct in a

few months, whereas long-lived species would be less affected. Population instability and the

probability of local extinctions is much greater for short-lived species than it is for long-lived

species (Pimm 1991). Thus, those aspects of a species life history that contribute to life

expectancy and lifetime reproductive potential should be considered when predicting the effects

of habitat fragmentation on a species.

Ecological Model Systems or Behavioral Model Systems?

What makes a good ecological model system? The EMS concept was first described by Ims and

Stenseth (1989) and later by Ims et al. (1993) and Wiens et al. (1993), but has had little

application to natural systems. If voles are to be used as EMS's, for what systems are they good

models? Voles, per se, probably are not good models for anything but voles. The problem has

been that researchers have been studying voles or other species and have not addressed the

attributes of a species that makes them an EMS for other systems. Voles are not good ecological

models for capercaillie grouse and mice are not good models for moose or any other species.

The argument that I make above is that certain *aspects of behavior* are the feature that is the

model that can be used to predict how another model system will respond in a similar situation.

For instance, voles are not good ecological models for capercaillie grouse, but territoriality is the

common feature that makes both species respond the same way to fragmentation (Ims et al.

1993). Similarly, voles are not good ecological models for brown bears, but the reason they have

similar colonization potential is that both species have female philopatry and male-biased

dispersal. In contrast, snowshoe hares and porcupines have greater colonization potential than

predicted by their body size because they are not territorial and females disperse as often and far

as do males. The common feature of ground squirrels, naked mole rats (*Heterocephalus glaber*),

and mountain sheep is their sociality or conspecific attraction that inhibits individual dispersal.

Thus, behavioral models systems (BMS) might be a more appropriate concept than the EMS's

and research should be designed to test hypotheses regarding the role of specific behavioral

systems in dispersal and response to fragmented landscapes.

The relative influence of the above BMS factors on the ability for mammal species to

colonize fragmented landscapes is summarized in Table 2. Specific examples for how each of

these parameters is predicted to affect the propensity for various representative mammal species

to colonize patchy habitats is presented in Table 3. The various parameters are presented as their

relative contribution to whether or not a given species is more or less likely to disperse and

successfully colonize and persist in a patch of habitat than is predicted by body size alone

(Appendix 1, Table 1). The values for each factor are expressed as + (positive = more likely to colonize), - (negative = less likely to colonize), or 0 neutral. The success of a species in colonizing habitat patches will be a function of the +/- ratio; with a higher value increasing the species chances for colonizing habitat patches. For instance, the red fox would be a good colonizer, the muskrat a poor colonizer, and the opossum intermediate. I compared the observed and predicted dispersal distances for 17 species from Appendix I that represent all trophic levels and a range of body sizes and life history traits (Table 3). Observed dispersal distances of 15 of these 17 species fit those predicted by the traits listed in the table. The five variables listed in Table 3 may not all be weighted the same, such as habitat specialist may have a greater influence on colonization potential than mode of life or sociality greater than trophic level. The list of variables and ranking is meant to be used as a relative ranking scheme to predict why some species should be better colonists than others.

Summary

I attempted to look for a general conceptual model to identify those features associated with a predisposition for a given mammal species to colonize new habitats. The overall pattern appears to be associated with various aspects of the species' evolutionary and natural history, degree of ecological specialization, trophic level, behavioral system, and body mass. Dispersal distance is a function of body mass, but also is influenced by ecological factors such as the distribution, predictability, and renewability of food resources and the type of habitat matrix between patches. Behavioral aspects that affect dispersal, colonization, and persistence are territoriality, sex-biased dispersal, and degree of sociality or conspecific attraction. These features should in turn affect

home range size and(or) annual movements. In species that have a predictable and(or) stationary and renewable food source, females appear to be relatively philopatric and are not adapted to long range movements or colonization of vacant habitats. Species that are adapted for colonizing new habitats are likely those that have evolved under conditions that require long-distance movements within the lifetime of individuals. These conditions should include seasonally available food (e.g. winter and summer range) and(or) unpredictable or a mobile food source, and frequent habitat disturbance such as early successional or fire-regime habitats.

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Table 1.

Allometric relationships between dispersal distance and body mass of mammals

(data are from Appendix 1).

Formula for dependent variable = ab^x where a = constant, b = mass, x = slope

Log(dispersal distance in km) = log(body mass in grams) x slope + intercept.

Trophic status	N	intercept ($\pm$ SE)	Slope ($\pm$ SE)	r^2	P
Carnivores	23	-1.369 ± 0.389	0.761 ± 0.109	0.701	<.001
Herb/omnivores	51	-1.375 ± 0.126	0.597 ± 0.040	0.907	<.001
All mammals	74	-1.420 ± 0.150	0.670 ± 0.045	0.868	<.001
Males	22	-1.095 ± 0.207	0.638 ± 0.065	0.828	<.001
Females	17	-1.769 ± 0.306	0.720 ± 0.103	0.767	<.001

Table 2.

Characteristics of species that make them good or poor colonizers of fragmented landscapes as

measured by dispersal ability.

Life, behavioral characteristics	Dispersal ability
Mode of life	aerial > terrestrial > arboreal > fossorial > freshwater
Degree of specialization	generalists > specialists
Spacing behavior	nonterritorial > territorial
Sex	females = males
Body size	large > small
Trophic level	carnivores > omnivores > herbivores
Mobility	migratory > nonmigratory
Sociality	asocial > social (conspecific attraction)

Table 3.

The relationship between the potential for colonization of representative terrestrial mammal species and

behavioral, ecological, and life history traits.

Species	Habitat generalist/ specialist	Trophic level	Mode of life	Sociality	Dispersing sex	Overall rating	Observed dispersal distance	Predicted disersal distance
deer mouse	+	0	+	+	-	+++	1.0	0.2
meadow vole	-	-	+	+	-	++	0.1	0.4
red squirrel	-	-	-	+	+	++	1.0	1.2
pika	-	-	+	+	0	++	0.05	0.9
white-tailed prairie dog	+	-	+	-	-	+	2.7	2.9
muskrat	-	-	-	-	-	-	.5	2.9
striped skunk	+	0	+	+	+	++++	12	4.6
marten	+	+	+	+	-	++++	45	9.4
opossum	+	0	+	+	-	+++	4.9	4.6
raccoon	+	0	+	+	-	+++	23	8

black-tailed deer	+	-	+	+	-	+++	26	31
bighorn sheep	-	-	+	-	-	+	46	40
ermine	+	+	+	+	-	++++	7	2.6
porcupine	+	-	0	+	+	++++	10	9
red fox	+	+	+	+	+	+++++	46	29
coyote	+	+	+	+	+	+++++	116	67
gray wolf	+	+	+	+	+	+++++	128	128

Habitat: generalist (+), specialist (-)

Trophic level: carnivore (+), omnivore (0), herbivore (-)

Mode of life: terrestrial (+), arboreal (-), fossorial (-), freshwater aquatic (-)

Sociality: asocial (+), social (-)

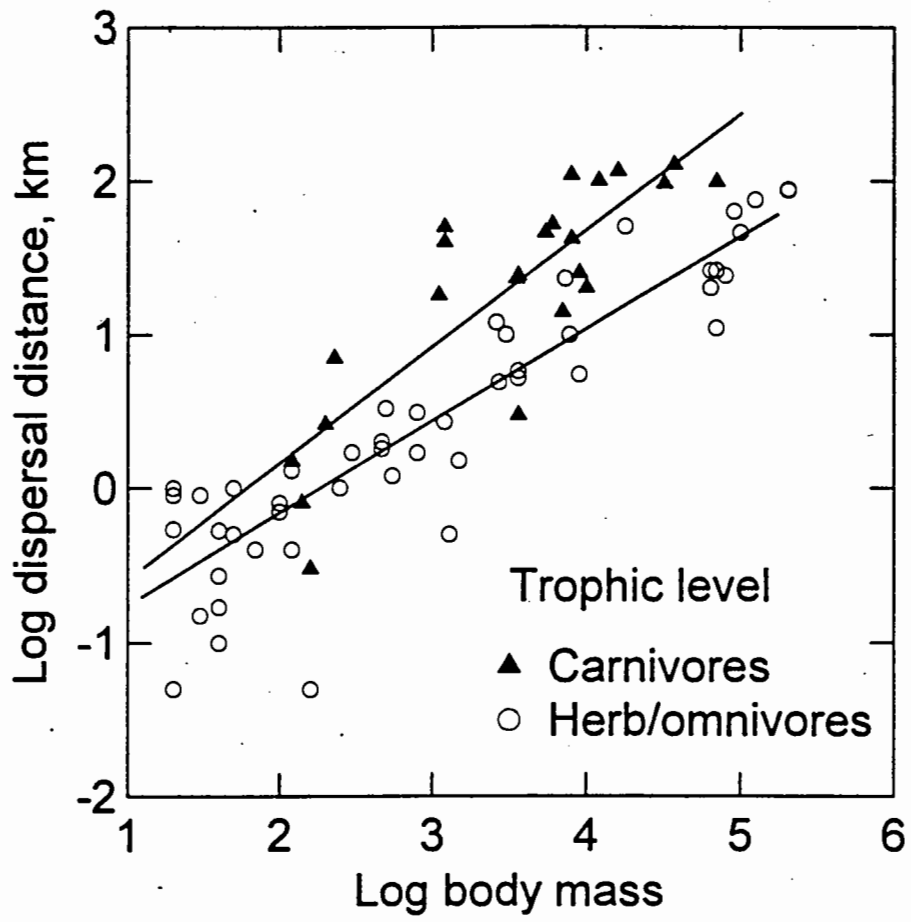Dispersing sex: females (or both sexes +), males (-)

Overall rating for potential to colonize (based on predicted dispersal distance as a function of body size): number of +'s indicate potential for colonization (poor 0 to good +++++)
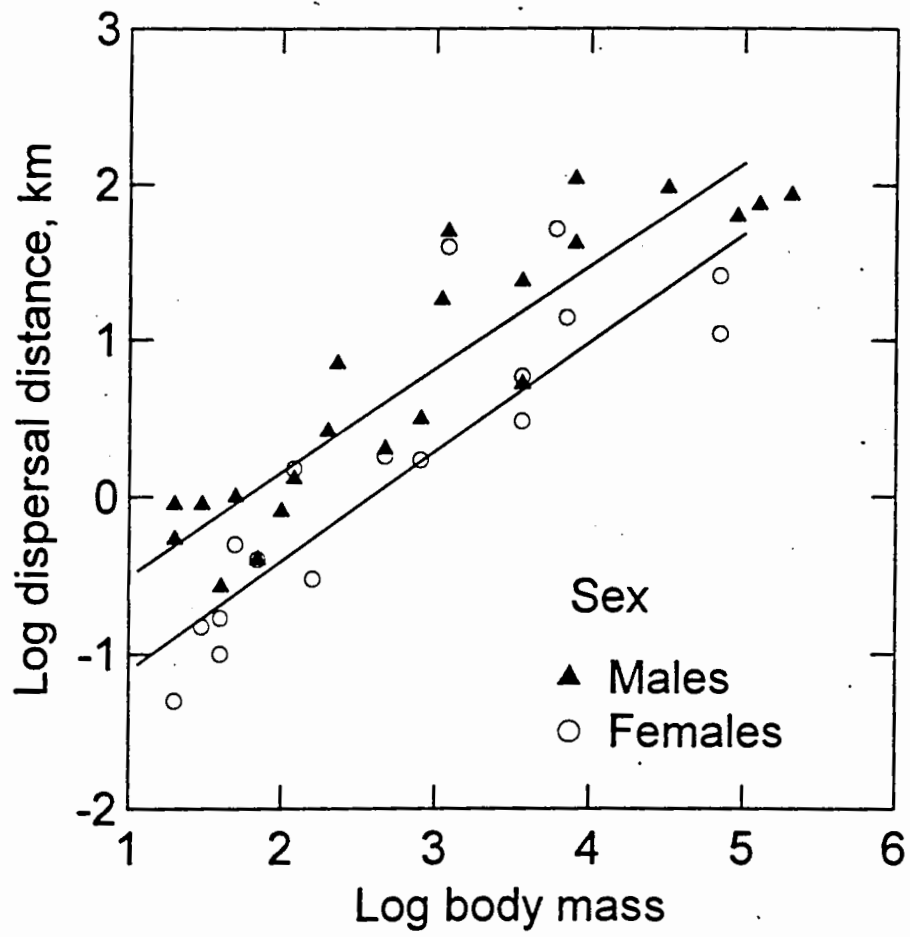
Observed and predicted dispersal distances are from Appendix I and formulas in Table 1.

List of Figures

Trophic level
▲ Carnivores
○ Herb/omnivores

Appendix 1.

Mean body mass, mean dispersal distance, and primary dispersing sex (M = males, F = females, B = both sexes, ? not reported) for 59

species of mammals.

Species	Sex	Mass kg	Mean distance km	Primary dispersing sex	References
Herbivores					
Field vole, *Microtus arvalis*	F	.02	0.05	M	Boyce and Boyce 1988
Field vole, *Microtus arvalis*	M	.02	0.54	M	Boyce and Boyce 1988
Bank vole, *Clethrionomys glarelous*	M	.02	1.0	M	Steen 1994
Field mouse, *Apodemus agrarius*	M&F	.02	1.0	M	Szaki and Liro 1991
Deer mice, *Peromyscus maniculatus*	M&F	.02	1.0	M	Burt 1940
Cotton mouse, *Peromyscus gossypinus*	M	.02	0.9	M	Pournelle 1950

Cotton mouse, *Peromyscus gossypinus*	F	.02	0.15	M	Pournelle 1950
Meadow vole, *Microtus pennsylvanicus*	F	.04	0.1	M	McShea and Madison 1992
Least chipmunk, *Tamias minimus*	M&F	.04	0.53	M	Meredith 1974
Yellow pine chipmunk *Tamias amoenus*	M	.05	1.0	M	Meredith 1974
Yellow pine chipmunk *Tamias amoenus*	F	.05	0.5	M	Meredith 1974
Merriam's kangaroo rat					
Dipodomys merriami	M	.04	0.27	B	Jones 1989
Merriam's kangaroo rat					
Dipodomys merriami	F	.04	0.17	B	Jones 1989
Stephen's kangaroo rat,					
Dipodomys stephensi	M	.07	0.4	B	Price et al. 1994
Stephen's kangaroo rat,					
Dipodomys stephensi	F	.07	0.4	B	Price et al. 1994
Taiga vole, *Microtus xanthognathus*	M	.1	0.8	M	Wolff and Lidicker 1980
Water vole, *Arvicola terrestris*	M	.12	1.3	M	Leuze 1980
Banner-tailed kangaroo rat					

Species	Sex				Reference
Dipodomys spectabilis	M&F	.12	0.5	B	Jones et al. 1988, Waser and Jones 1989, Amarasekare 1994
Pika, *Ochotona princeps*	M&F	.16	.05	B	Smith and Ivins 1983
Red squirrel, *Tamiasciurus hudsonicus*	M&F	.25	1.0	B	Price and Boutin 1993
Red squirrel, *Sciurus vulgaris*	M&F	.3	1.7	M	Wauters et al. 1994
Pocket gopher, *Thomomys talpoides*	?	.1	0.8	B	Vaughan 1963
Valley pocket gopher, *Thomomys bottae*		.1	0.7	B	Lidicker and Patton 1987
Columbian ground squirrel					
Spermophilus columbianus	F	.47	1.8	M	Hackett 1987, Wiggett and Boag 1989
Columbian ground squirrel					
Spermophilus colombianus	M	.47	2.0	M	Hackett 1987, Wiggett and Boag 1989
California ground squirrel,					
Spermophilus beecheyi	M&F	.6	1.2	M	Evans and Holdenreid 1943
E. Gray squirrel, *Sciurus carolinensis*	M&F	.5	3.3	M	Cordes and Barkalow 1972

52

Species	Sex	Col1	Col2	Type	Reference
Fox squirrel, *Sciurus niger*	?	.8	1.2	M	Baumgartner 1938
Fox squirrel, *Sciurus niger*	?	.8	16.1	M	Allen 1943
Black-tailed prairie dog, *Cynomys ludovicianus*	M	.8	3.1	M	Garrett and Franklin 1988
Black-tailed prairie dog, *Cynomys ludovicianus*	F	.8	1.7	M	Garrett and Franklin 1988
White-tailed prairie dog *Cynomys leucurus*	M&F	1.2	2.7	M	Clark et al. 1971
Muskrat, *Ondatra zibethicus*	?	1.2	0.5	M	Beshears 1951, Errington 1951
Snowshoe hares, *Lepus americanus*	M&F	1.5	1.5	B	O'Donoghue and Bergman 1992, Keith et al. 1993
Striped skunk, *Mephitis mephitis*	M&F	2.6	10-12	B	Sargeant et al. 1982
Opossum, *Didelphis virginiana*	M&F	2.7	3.2-4.9	B	Van Druff 1971
Opossum, *Didelphis virginiana*	M	2.7		B	Reynolds 1945
Mountain hare, *Lepus timidus*	?	3.0	10	B	Hewson 1990
Marmot, *Marmota flaviventris*	M	3.6	5.2	M	Salsbury and Armitage 1994, VanVuren and Armitage 1994

Marmot, *Marmota flaviventris*	F	3.6	5.8	M	Salsbury and Armitage 1994, VanVuren and Armitage 1994
Porcupine, *Erethizon dorsatum*	M&F	7.8	10	B	Dodge and Barnes 1975, Marshall et al. 1962
European badger, *Meles meles*	M	9	4.5	M	Cheeseman et al. 1988
European badger, *Meles meles*	F	9	5.5	M	Cheeseman et al. 1988
Raccoon, *Procyon lotor*	M&F	7	23	M	Giles 1943, Priewert 1961, Lynch 1967, Fritzell 1978
Beaver, *Castor canadensis*	M&F	18	50	B	Beer 1955, Libby 1957, Hodgdon 1978, Chubbs and Phillips 1994
Black-tailed deer, *Odocoileus hemionus*	M&F	64	26	M	Brown 1961, Bunnell and Harestad 1983
Mule deer, *Odocoileus hemionus*	M&F	64	20	M	Brown 1992
White-tailed deer, *Odocoileus virginianus*	M&F	91	63	M	Nelson and Mech 1992, Nelson 1993, Nixon et al. 1994
Mountain goat, *Oreamnos americanus*	M&F	80	24	B	Richardson 1961

Bighorn sheep, *Ovis canadensis*	M&F	1.00	46	M	Welles and Welles 1961, Spalding and Mitchell 1970
Black bear, *Ursus americanus*	F	70	11	M	Rogers 1987
Black bear, *Ursus americanus*	M	125	75	M	Rogers 1987
Grizzly bear, *Ursus arctos*	M	204	87	M	Craighead 1980
Elk, *Cervus elaphus*	M&F	204	88	M	Brazda 1953, Cole 1969

Carnivores

Townsend's mole, *Scapanus townsendii*	M&F	.14	.8	B	Giger 1973
Ermine, *Mustela erminea*	F	.12	1.5	M	Erlinge 1977
Ermine, *Mustela erminea*	M	.23	7	M	Erlinge 1977
Wambenger, *Phascogale tapoatafa*	F	.16	.3	B	Soderquist and Lill 1995
Wambenger, *Phascogale tapoatafa*	M	.2	2.6	B	Soderquist and Lill 1995
Mink, *Mustela vison*	M	1.1	18	M	Mitchell 1961; Gerell 1970

Species	Sex				Reference
Marten, *Martes americana*	M	1.2	40	M	Hawley and Newby 1957
Marten, *Martes americana*	F	1.2	50	M	Latour et al. 1994
Fisher, *Mustela pennanti*	F	2.3	22.6	M	Arthur et al. 1993
Fisher, *Mustela pennanti*	M	4	23.0	M	Arthur et al. 1993
Gray fox, *Urocyon cinereoargenteus*	M	3.6	24	B	Nicholson et al. 1949
Gray fox, *Urocyon cinereoargenteus*	F	3.6	3	B	Nicholson et al. 1949, Sheldon 1953
Red fox, *Vulpes vulpes*	M&F	5.4	46	B	Pils and Martin 1978, Trewhella et al. 1988, Allen and Sargeant 1993, Zimen 1984
American badger, *Taxidea taxus*	F	6	52	M	Messick and Hornocker 1984
American badger, *Taxidea taxus*	M	8	110	M	Messick and Hornocker 1984
Otter, *Lutra lutra*	M	8	16	M	Erlinge 1968
Otter, *Lutra canadensis*	F	7	14	M	Melquist and Hornocker 1983
Otter, *Lutra canadensis*	M	8	42	M	Melquist and Hornocker 1983

Species					References
Bobcat, *Felis rufus*	M&F	9	25	M	Rollings 1945; Erickson 1955; Robinson and Grand 1958; Knick 1990
Lynx, *Felis lynx*	M&F	10	20	M	Saunders 1963; Nellis and Wetmore 1969; Mech 1977
Wolverine, *Gulo gulo*	M&F	12	100	B	Magoun 1985, Gardner et al. 1986
Coyote, *Canis latrans*	M&F	16	116	B	Bekoff 1982; Bowen 1982; Harrison 1992
Sea otter, *Enhydra lutris*	M	32	96	M	Jameson 1979
Gray wolf, *Canis lupus*	M&F	37	128	B	Kelsall 1968; Mech 1970; van Camp and Gluckie 1979; Ballard et al. 1983; Gese and Mech 1991; Mech et al. 1995
Cougar, *Felis concolor*	M&F	70	99	M	Hemker et al. 1965; Beier 1995

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16. Abstract:
The impact of habitat loss and fragmentation of remaining habitats on the viability of plant and animal species is a major concern in conservation biology and landscape ecology. Because experimental and observational data on species responses to habitat loss and fragmentation are costly to collect, and impossible to collect for rare, endangered, and large species, "ecological model species" (EMS) are frequently used to predict how other species will respond to these disturbances. For example, experimental studies using small mammals (e.g., voles) in enclosed or manipulated habitats have been used to predict how other species (e.g., cougar or grouse) might respond to similar situations. Unfortunately, little attention has been paid to what attributes make a given species an appropriate EMS for other species. Dr. Jerry Wolff, onsite cooperator from Oregon State University at NHEERL's Western Ecology division, reviewed the available literature on species' response to habitat fragmentation and potential for habitat colonization. Based on this evidence, he concludes that certain aspects of behavior play a major role in determining how species respond to fragmented landscapes and that "behavioral model systems" might be a more appropriate basis, than the EMS concept, for making comparisons and predictions among species. Dr. Wolff found that behavioral traits, such as mobility, territoriality, sex-biased dispersal, mode of life (aerial, terrestrial, arboreal, fissural, freshwater,) degree of specialization, degree of sociality or conspecific attraction, and trophic level, were related in a consistent and predictable manner to the potential for a species to colonize fragmented habitats. The Pacific Northwest Research Program at WED is evaluating the effects of large-scale landscape change on terrestrial vertebrate biodiversity, as well as other ecological endpoints. The "behavioral model system" proposed in this paper will be used eventually to improve model predictions of species viability and the effects of habitat loss and fragmentation in the Northwest on terrestrial biodiversity.

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