EFFECTS OF FOOD AND ECTOPARASITES ON AGE OF NATAL DISPERSAL IN BURROWING OWLS

by

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DEDICATION

This thesis is dedicated to my parents, Flori and Divo Garcia

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ABSTRACT

Variation in the age that juveniles disperse appears to be common in animals, yet the reason for this variation has rarely been examined. I examined how food and ectoparasites influenced age of natal dispersal in burrowing owls (*Athene cunicularia*). I radio-collared juvenile burrowing owls at 135 nests in eastern Washington from May to October of 2002 and 2003. I assigned each nest to a food-supplemented or control group, and an ectoparasite-reduction or control group. I estimated relative abundance of food surrounding a subset of nests by trapping small mammals. I also estimated relative abundance of ectoparasites by assigning each juvenile an index of flea load. Mean dispersal age was 73 days old (n = 98) but differed between the 2 study years ($\#_{2002}$ = 66 days compared to $\#_{2003}$ = 80 days; 95% CI: 59-72 and 73-86, respectively). Small mammals were more than twice as abundant in 2003 compared to 2002, and juveniles responded differently to the treatments each year. Food supplements had an effect on dispersal age in 2002 but not in 2003, and ectoparasite reduction had an effect in 2003 but not 2002. In 2002, food-supplemented juveniles initiated dispersal 10 (95% CI: -18 – -1) days younger than controls. In 2003, juveniles treated for ectoparasites initiated dispersal 15 (95% CI: -27 – -2) days younger than controls. I found no influence of ambient food or flea load on dispersal age either year. Food and ectoparasites both influence dispersal age, but the influence is context-dependent.

INTRODUCTION

Dispersal influences many ecological and evolutionary processes (Gandon and Michalakis 2001). Dispersal results in gene flow among populations, and thus the frequency of dispersal events affects population dynamics, speciation, and the ability to adapt to local environments (Greenwood 1980, Johnson and Gaines 1990, Clobert et al. 2001). Natal dispersal (movement from the natal site to the site of the first breeding attempt) is distinguished from breeding dispersal (movement from the site of one breeding attempt to the site of the next breeding attempt; Greenwood 1980). In many taxonomic groups, natal dispersal occurs more commonly and involves longer movements than breeding dispersal and thus has been assumed to play the major role in gene flow, population structure, and connectivity (Greenwood and Harvey 1982, Payne 1990, Dale et al. 2004).

Although natal dispersal is common, leaving the natal area for the first time can be risky (Nilsson and Smith 1985) and probably evolved to avoid the negative consequences of inbreeding or competition among kin (Greenwood 1980, Greenwood and Harvey 1982, Johnson and Gaines 1990, Ferrer 1992, Alonso et al. 1998). One way to potentially reduce some of the risks associated with dispersal is to delay departure from the natal area (Ekman et al. 2004). Delayed natal dispersal is not uncommon and is considered a precursor to the evolution of kin-based cooperative breeding (Brown 1974, Gaston 1978, Emlen 1982, Gardner et al. 2003). The timing when young leave their natal area may also influence survival and the ability of young to find a suitable breeding territory (Brewer and Harrison 1975, Morton et al. 1991, Morton 1992). Because when

natal dispersal is initiated appears to have important fitness consequences, we would expect strong selection on the age that juveniles initiate natal dispersal (hereafter referred to as dispersal age). Nevertheless, dispersal age varies among species, populations, and individuals within a population (Drent 1984, Nilsson and Smith 1985, Yoerg 1998, Russell 2000, Russell et al. 2004), perhaps because the relative benefits of early or late dispersal are context-dependent.

Dispersing early may facilitate territory acquisition when the outcome of competition for vacant territories is primarily determined by who arrived first (Drent 1984, Nilsson and Smith 1988). For example, early dispersers may be able to secure the northernmost winter territories, thereby arriving at their breeding territories earlier in the spring and increasing their chances of obtaining a mate or territory. In non-migrants, early dispersers may have a greater choice of territories near the natal area than later dispersers (Yoerg 1998). Early dispersal is also beneficial if food abundance decreases throughout the breeding season. Young who disperse while food is still abundant may have higher survival compared to young that delay dispersal until food has become scarce because dispersing juveniles often travel through unfamiliar areas in which food must be procured without prior knowledge of availability. The likelihood of finding food in unfamiliar areas is presumably greater if food abundance is higher in the landscape.

In situations where early dispersal is the best strategy, juveniles in better condition or with more access to resources would be expected to disperse earlier than others, which has been observed in some populations. For example, juvenile marsh tits (*Parus palustris*) that dispersed earlier were larger than later-dispersing siblings (Nilsson

and Smith 1985). Juvenile Mexican spotted owls (*Strix occidentalis lucida*) that were supplemented with food dispersed earlier than controls (Willey and van Riper III 2000). Dominant juvenile Western screech owls (*Otus kennicottii*) dispersed before subordinate siblings (Ellsworth 1997).

In contrast, delayed natal dispersal might be the best strategy in some environments. Remaining in the natal area may allow juveniles to practice foraging in an area with which they are familiar (Yoerg 1998). Delayed dispersal may allow juveniles to refrain from competing with conspecifics until they have more foraging experience or until food conditions improve (Yoerg 1998, Ekman et al. 2004). If juveniles vary in social status, subordinate juveniles may be forced to delay dispersal to attain adequate condition prior to dispersal (Nilsson and Smith 1985, Ellsworth and Belthoff 1999).

If delaying dispersal were beneficial, juveniles in areas with higher food abundance, food-supplemented juveniles, and dominant juveniles would be expected to disperse older or later. Indeed, male goshawks (*Accipiter gentilis*) in areas with greater food abundance dispersed older than those in areas with less food (Kenward et al. 1993). Food-supplemented goshawks of both sexes and red kites (*Milvus migrans*) initiated natal dispersal later than controls (Kenward et al. 1993, Bustamante 1994). Dominant juvenile gray jays (*Perisoreus canadensis*) apparently dispersed later than subordinates (Strickland 1991). Hence, the effect of food abundance on dispersal age appears to vary depending on other selective pressures. Optimal dispersal age may even differ between sexes within the same population (Kenward et al. 1993, Alonso et al. 1998) if males and females differ in the proximate or ultimate causes for dispersal (Greenwood 1980).

Proximate factors that influence variation in dispersal age potentially include parent-offspring conflict (Trivers 1974), in the form of aggression (Alonso et al. 1987, Hiraldo et al. 1989) or decreased parental provisioning (Davies 1976, Delannoy and Cruz 1988, Gjerdrum 2004), or sibling aggression (Strickland 1991). Other proximate cues may involve internal mechanisms such as the acquisition of some critical skill (e.g., foraging ability; Brown 1987, Langen 1996), reaching a critical threshold in growth (e.g., wing length; Kenward et al. 1993, Deguchi et al. 2004), or increased hormone levels (Belthoff and Dufty 1998). We know less about when and how ultimate factors (e.g., food abundance) influence variation in dispersal age.

Burrowing owls (*Athene cunicularia*) are a good species in which to examine the factors influencing intraspecific variation in dispersal age because individuals within the same population vary widely in the age at which they disperse. I have observed that some individuals disappear from the natal area soon after they are able to fly (~40 days old), whereas others remain in the natal area until their plumage and behavior are indistinguishable from those of adults (≥100 days old).

In birds, the post-fledging period (i.e., when dispersal is initiated) is often the life stage with the lowest daily survival probability (Nilsson and Smith 1985, Gill 1995). Juvenile birds are particularly vulnerable during dispersal because they must forage and evade predators without the benefit of parental care. Thus, inexperienced juveniles are at greater risk of mortality via predation and starvation than adults in most taxa (Gill 1995). Indeed, mortality is often highest during the post-fledging period in burrowing owl populations (Todd 2001a).

Burrowing owls are an endangered species in Canada and are listed as a *Bird of National Conservation Concern* in the United States (Klute et al. 2003). In Washington (where my study was located), burrowing owls are a *State Candidate* for listing as *Endangered, Threatened or Sensitive*. Understanding the processes that influence dispersal age will provide agencies with information needed to better manage populations. Large variation in dispersal age may be due to variation in food abundance, burrow density, volume of the natal burrow, ectoparasite abundance, CO_2 build-up in the natal burrow, or predator density. I tested 2 of these alternative hypotheses (food abundance and ectoparasite infestation) in an attempt to explain why burrowing owls vary in dispersal age. If lack of food or flea-infested burrows influence dispersal age and thereby expose owls to increased predation or starvation, supplementing food or insecticide during a critical period may increase survival and/or local recruitment of burrowing owls.

My thesis research focused on 4 objectives: 1) to determine the effect of food supplementation on dispersal age, 2) to determine the effect of reducing ectoparasites in the nest burrow on dispersal age, 3) to determine the relationship between food abundance surrounding the nest burrow and dispersal age (in non-supplemented burrows) and, 4) to determine the relationship between flea load and dispersal age in burrowing owls.

Food abundance hypothesis

If food abundance is high, juveniles may experience accelerated growth, weight gain, or fat storage. Therefore, juveniles may attain the size or body condition at which they would normally disperse sooner when food abundance is high. Thus, if early dispersal is the best strategy, juveniles in areas of high food abundance might disperse sooner than juveniles in areas of low food abundance. Alternatively, juveniles may be favored to remain in the natal area as long as conditions are favorable (i.e., to delay dispersal). In that case, juveniles in areas of high food abundance may opt to remain in their natal territory longer so that they can grow or put on body fat in a familiar foraging area. Therefore, high food abundance may facilitate either early or delayed dispersal. I examined the effect of food on dispersal age by using both an experimental and an observational approach.

Ectoparasite abundance hypothesis

Nestling burrowing owls are often infested with ectoparasites (mostly fleas and lice; Smith and Belthoff 2001). High ectoparasite load may be a harmless, temporary by-product of burrow life. However, fleas and other ectoparasites negatively affect reproductive success of avian hosts in a variety of ways (Møller 1997). In birds, fleas and ectoparasites have been associated with lower nestling body mass (Brown and Brown 1992, Christe et al. 1996), decreased nestling survival (Brown and Brown 1986), differences in recruitment to the natal colony (Brown and Brown 1992), differences in natal dispersal distance (Heeb et al. 1999), and colony abandonment (Loye and Carroll

1991). Additionally, some flea species (*Pulex irritans* and *Aetheca wagneri*) found on burrowing owls are important vectors of plague (Smith and Belthoff 2001). To my knowledge, the effect of fleas on burrowing owls has not been studied, and the effects of ectoparasites on natal dispersal decisions are not well known (Boulinier et al. 2001). If ectoparasites are harmful, we might expect juveniles with heavy ectoparasite infestation to disperse later. One possible mechanism could be that juveniles with heavy ectoparasite infestation might have to allocate increased energy toward immune system functions, and thereby have less energy available for growth than juveniles with few or no ectoparasites. Alternatively, if ectoparasites were harmful to owls but owls were still able to grow normally, we might expect heavily infested broods to disperse earlier in an attempt to escape their infested nest burrows. I used both an experimental and an observational approach to examine the effects of ectoparasites on dispersal age in burrowing owls.

STUDY AREA

My study area covered approximately 3600 km^2 of sagebrush steppe in the Columbia Basin of eastern Washington (Grant and Adams counties; Fig. 1). The primary land use in the area was irrigated croplands but also included pasture, urban, suburban, and undisturbed areas. Elevation varied from 316-398 m above sea level, and annual precipitation in the area is usually <25 cm, which falls primarily as rain from October to May (Blackwood et al. 1997). I conducted the fieldwork from May to October of 2002

and 2003. Most burrowing owls in this area of Washington are migratory (Conway et al. 2003).

METHODS

Locating and monitoring nests

I located nests by conducting roadside surveys (Conway and Simon 2003), by visiting burrows where local resource managers or property owners had seen burrowing owls in the past, and from incidental sightings. I visited each nest (n = 135) once or twice a week to collect nesting and behavioral data. I excluded nests that were on the periphery of the study area ($n \approx 10$) because they were too far to be visited every 2 days for radio tracking (see *Determining dispersal age* below). Additionally, I excluded nests that had human-made structures nearby ($n \approx 5$) that interfered with the radio signal, nests that were not regularly monitored due to lack of permission from property owners ($n \approx 7$), and nests that were found too late in the nesting cycle to determine hatch date ($n \approx 13$). Finally, I excluded nests ($n \approx 4$) from those analyses that required estimates of dispersal age if I was unsuccessful at trapping juveniles or juveniles emerged after I had used all the transmitters I was permitted to use each season. All methods were approved by the Washington Department of Fish and Wildlife, the U.S. Fish and Wildlife Service, and the University of Arizona's Institutional Animal Care and Use Committee (approved protocols #01-089 and #03-052).

Determining dispersal age

I determined dispersal age by trapping juveniles (Conway and Garcia 2005) and placing a 4.6-g radio transmitter (Model PD-2C, Holohil Systems Ltd., Ontario, Canada) on 1 juvenile burrowing owl in each brood. If a radio-collared juvenile died, I attempted

to trap and radio-collar a sibling from the same brood. Thus, I radio-collared 170 juveniles (87 in 2002 and 83 in 2003) from 135 broods (67 in 2002 and 68 in 2003). I attempted to locate radio-collared juveniles every 2-3 days using a handheld 3-element Yagi antenna.

When I could not locate a juvenile after 4 days using the handheld antenna, I used a vehicle-mounted whip antenna and scanned for the missing signal throughout a 3.2-km^2 area surrounding the location where that juvenile was last detected. If vehicular scans were unsuccessful, I attempted to locate juveniles via aerial tracking over and slightly beyond the entire study area. I flew in a Super Cub or Maule airplane with an H-antenna attached to the wing strut of each wing. I flew transects 1.9 km (1 min lat/long) apart at an altitude of 305 m in 2002, and transects 11 km apart (6 min lat/long) at 1707 m in 2003. If I detected the signal of a missing juvenile from the plane, I later tried to locate the bird on the ground. I scanned frequencies of all missing juveniles each time I flew throughout the season. In 2002, I flew 12 times between 2 Aug and 5 Oct and covered the entire study area within 1 or 2 days. In 2003, I flew 10 times between 25 Jul and 21 Oct and was able to cover the study area within 1 day. These flights allowed me to locate ~38 owls that I had been unable to locate from the ground.

If I could not detect the signal of a missing juvenile using any of these methods, I assumed the juvenile had initiated dispersal and moved away from the study area. I also assumed a juvenile had initiated dispersal when the juvenile roosted >300 m (King and Belthoff 2001) away from the natal burrow for 2 or more consecutive visits. If the signal disappeared from the natal area (within 300 m of the nest burrow) but the juvenile was

dead by the time I re-located the signal, I considered the juvenile to have dispersed if the remains were >2 km from the nest. I assumed juveniles found dead >2 km from their nest initiated dispersal because I assumed that a predator would be unlikely to kill an owl at the owl's nest, then travel >2 km before consuming the owl and leaving the remains where I found them. Other causes of death, such as starvation or collision with a vehicle, also probably occurred near where the juvenile was found dead rather than at the nest burrow. This assumption rests on a second assumption: that juvenile burrowing owls that traveled >2 km from their nest were not going to return to their nest. That is, if a juvenile was traveling when killed, and was killed >2 km from its nest, the juvenile was not likely to return to the nest burrow. However, even if this assumption is incorrect, only 14 juveniles were found dead away from their nest, 8 of which were >2 km from their nest and 6 of which were >300 but <2 km from their nest.

I estimated dispersal date for each radio-collared juvenile by taking the mid-point between the last date the juvenile was present in the natal area and the first date the signal was not detected within the natal area. I calculated each juvenile's age on the date they dispersed by subtracting their estimated hatch date (see *Hatch date* below) from the estimated dispersal date.

Covariates

To isolate the effects of food and ectoparasites, I measured 3 intrinsic factors that I thought might influence dispersal age: hatch date, parental departure, and sex. If any of these variables explained a significant amount of variation in dispersal age, I controlled

for the effect of the variable by including the variable as a covariate in the statistical analyses.

Hatch date

I estimated hatch date of juvenile owls using a combination of information obtained during weekly nest visits and trapping. Hatch dates were based on observing partial and final clutch sizes using an underground infrared probe and then using burrowing owl breeding cycle phenology to calculate hatch date (Garcia and Conway, unpubl.). If I could not access the nest chamber using the infrared probe, I used a photographic and descriptive ageing guide (modified from Priest 1997) to calculate hatch date by ageing juveniles when they emerged from the burrow or when I trapped them, and counting backwards to determine the hatch date. I worked with others to develop a standardized protocol for estimating hatch date of juveniles based on observations during nest visits (Garcia and Conway, unpubl.).

Parental departure

I examined the relationship between dispersal age and parental departure. I examined 4 measures of parental departure to determine which explained the most variation in dispersal age: age of the radio-collared juvenile on the date the 1) adult male, 2) adult female, 3) first parent to depart, and 4) second parent to depart left the natal area. I determined departure dates of parents by taking the mid-point between the last nest visit that the parent was present in the natal area and the first nest visit that the parent was not

seen for ≥3 nest visits. Parental departure could not be determined for 1 nest in 2002, so I excluded that nest from analyses that included parental departure.

Sex

Juvenile burrowing owls are sexually monomorphic. To assess whether dispersal age differed between males and females, I collected blood from the brachial vein of each radio-collared juvenile. I submitted blood samples of juveniles that dispersed to Arizona Research Laboratories, University of Arizona, for analysis. The laboratory determined the sex of each juvenile by extracting DNA, running a polymerase chain reaction (PCR) optimization to test the primers using known-sex birds, and then running each sample through a PCR and gel electrophoresis. The procedure for use in burrowing owls (Appendix A) was modified from Fridolfsson and Ellegren (1999) by Dr. Mairi MacKay, Dept. of Biological Sciences, University College of the Cariboo, Kamloops, BC.

Supplementing food and treating for ectoparasites

I experimentally assessed the effects of food abundance and ectoparasite load on dispersal age of burrowing owls by assigning 2 treatments to nests in a full factorial arrangement with a completely randomized design. The first treatment consisted of supplementing nests with dead laboratory mice. I attempted to provide each family in the food-supplemented group of nests with at least 50% of the family's weekly energetic needs. Each food-supplemented nest was provisioned with at least 95 g of food per owl every 7 days (i.e., ≥13.6 g of food per owl per day). On average, adult burrowing owls in

captivity consumed 26.4 g (15.9% of their body weight) daily (Marti 1973). Lab mice were placed inside the entrance to burrow(s) that juveniles were using to minimize the possibility that owls from nearby nests could gain access to the supplemental food (Wellicome 2000).

The second treatment consisted of treating nests with an insecticide (diatomaceous earth powder without pyrethrin) to reduce ectoparasite loads. Diatomaceous earth has been used to control pests in organic farming (Stephens 1994, Agri-growth International Inc. 2004), food storage (Korunic 1998), and to control internal and external parasites in livestock (Wells 1999, Maine Organic Farmers and Gardeners Association 2004) and pets (Lyon 2000, Central Contra Costa Sanitary District 2002). Diatomaceous earth is used to control ectoparasites in chicken coops and chinchilla (*Chinchilla lanigera*) pens by making it available for dust baths (Agri-growth International Inc. 2004, McMurray Hatchery Inc. 2004). Recently, diatomaceous earth was found to reduce ectoparasites in tree swallow nests (Dawson 2004). I placed 79-118 ml of diatomaceous earth powder inside the entrance of each ectoparasite-treatment burrow so that owls could take a dust bath (Thomsen 1971) with the powder. I also sprayed the burrow tunnel 5 times (to saturate the dirt) with a solution made from diatomaceous earth powder and water (59ml diatomaceous earth/3.8L water; Garrett 2003).

I began providing laboratory mice and diatomaceous earth to nests in the 2 treatment groups when juveniles first emerged from their nest burrow (~14 days) and continued until juveniles dispersed from their natal area. I treated nests weekly during nest visits in which we approached all nests so that treatment and control nests received

on average the same number of visits. I compared dispersal age of radio-collared juveniles in treatment burrows with that of radio-collared juveniles in control burrows.

Measuring the effectiveness of treatments

To assess whether the treatments were effective in increasing access to food and reducing ectoparasites, I would have had to recapture juveniles when they were of (or just beyond) dispersal age and measure a variety of morphometric factors such as body mass, tarsus length, wing chord, feather growth, relative flea load, etc. However, burrowing owls are difficult to capture when they are older and I did not want to influence their dispersal behavior by attempting the intense trapping that would have been required at that age. Therefore, I did not recapture juveniles. I assessed treatment effectiveness indirectly by using data collected when I radio-collared juveniles to compare the treatment and control groups. When I captured juveniles to radio-mark them, I weighed them, estimated percent wing feather emergence (in 2002 only), and assigned them an initial index of flea load (see *Measuring relative flea load* below). I captured juveniles at a variety of ages, but began treating juveniles with lab mice and diatomaceous earth when they were about 14 days old. Hence, some juveniles were weighed and assigned an index of flea load after receiving only 1 treatment (food supplement and/or ectoparasite treatment), and others after receiving many treatments. Therefore, to evaluate the effectiveness of the food supplements, I examined the relationship between body mass and age captured (and between percent wing feather emergence and age captured) for both food-supplemented and control juveniles. If the food-supplements were effective, I

expected supplemented juveniles to gain body mass (or grow wing feathers) faster than control juveniles. Unlike food supplements, ectoparasite treatments probably produce an immediate rather than a cumulative effect. Therefore, to evaluate the effectiveness of the ectoparasite treatments, I compared flea load indices between juveniles treated for ectoparasites and controls.

Measuring relative small mammal abundance

Small mammals, including deer mice (*Peromyscus maniculatus*), make up ~90% of the total biomass in burrowing owl diets (Thompson and Anderson 1988, Green et al. 1993). I measured relative small mammal abundance surrounding nest burrows by trapping small mammals in Sherman live-traps baited with rolled oats and peanut butter (1:3 ratio, 11 ml per trap). I set 64 traps in an 8×8 grid with 15-m spacing centered on the nest burrow (Fig. 2). If an 8×8 grid was not possible due to an obstruction (e.g., a paved road), I set the traps in the closest possible configuration and maintained 64 traps. If the nest burrow could not be the center of the grid due to an obstruction ($n \approx 28$ of 51 nests), I set up the grid so that the burrow was as close to the center of the grid as possible. I marked captured rodents by clipping 1 ear tip or by cutting a patch of fur if ears were not visible. In 2002, I trapped small mammals at 35 of 36 nests that did not receive food supplements. In 2003, I trapped small mammals at 16 of 24 nests that did not receive food supplements. In both years, small mammal trapping resulted in greater disturbance at nests where I trapped small mammals than nests where I did not trap. However, within nests that did not receive food supplements in 2003, I compared dispersal ages at nests

where I trapped small mammals and those where I did not trap small mammals so that I could examine whether trapping influenced dispersal age. I trapped small mammals once when juveniles first emerged from the burrow (~14 days) and once after juveniles were past fledging age (~40 days). Trapping before and after fledging age allowed me to estimate relative small mammal abundance 2 times during the season which was important because owls may disperse in response to decreasing food at the end of the season, or they may disperse prior to the time when food availability declines (to avoid food stress). Traps were open for 2 nights during each of the 2 trapping sessions. I calculated relative small mammal abundance for the first trapping session alone, for the second trapping session alone, and for both trapping sessions combined (correlation between relative small mammal abundance from the first and second trapping sessions was $r = 0.478$, $P = 0.0004$, $n = 50$; Fig. 3). I did not have dispersal ages or parental departures for 13 nests where I trapped small mammals because juveniles at those nests died prior to dispersal. Therefore, I excluded those nests from analyses that contained dispersal age (and/or parental departure) and relative small mammal abundance as variables.

Measuring relative flea load

While radio-collaring juveniles, I assigned each juvenile an index of ectoparasite abundance (0-5) based on how many ectoparasites (usually fleas) were visible on the bird. Owls received a 0 if no ectoparasites were visible on the skin or feathers, a 1 if 1-2 ectoparasites were visible, a 2 if 3-6 ectoparasites were visible, a 3 if 7-10 ectoparasites

were visible, a 4 if 11-15 ectoparasites were visible, and a 5 if >15 ectoparasites were visible. Ten of 98 juveniles were captured and assigned an index of flea load more than once, so I used the average of the indices for these juveniles.

Statistical analyses

I used *t*-tests to compare mean dispersal age, mean hatch date, and mean dispersal date between the 2 study years (2002 and 2003), and to compare mean dispersal age between males and females. I used multiple linear regression to examine whether parental departure, hatch date, and sex were associated with dispersal age. I started by including all 3 covariates (parental departure, hatch date, and sex) in the model as explanatory variables and dispersal age as the response variable. I then excluded sex from the model because sex failed to explain a significant amount of the variation in dispersal age.

I used multiple linear regression to examine the effects of the 2 treatments on dispersal age. The explanatory variables were food treatment, ectoparasite treatment, parental departure, hatch date, and year (2002 or 2003), and the response variable was dispersal age. I initially included all two-way interactions between explanatory variables in the model and one 3-way interaction: food treatment × ectoparasite treatment × year. I used backwards elimination to exclude interactions that had *P*-values >0.20 from the model. After eliminating all the interactions with *P*-values >0.20, the only remaining interactions were all the 2-way interactions which included year: food treatment × year ($P = 0.042$), ectoparasite treatment × year ($P = 0.018$), parental departure × year ($P = 0.052$),

hatch date × year ($P = 0.049$). Because year interacted with all the explanatory variables, I also analyzed the 2 study years separately. Hence, the final model I used to examine the effects of the 2 treatments on dispersal age contained food treatment, ectoparasite treatment, parental departure, and hatch date as explanatory variables, and dispersal age as the response variable. Using this model, I present the results of the 2 study years separately as well as the 2 years combined.

To examine whether the food supplements were effective, I used multiple linear regression to compare the slopes of body mass (or percent wing feather emergence) vs. age between the food-supplemented and control groups. I used age, food treatment, and age × food treatment as the explanatory variables, and body mass (or percent wing feather emergence) as the response variable. I examined each year separately. To examine whether the ectoparasite treatments were effective, I used a *t*-test to compare the index of flea load between the ectoparasite-treated and control groups. I examined each year separately.

I used a *t*-test to compare dispersal age between nests that were not food-supplemented where I trapped small mammals and nests that were not food supplemented where I did not trap small mammals. I calculated an index of small mammal abundance surrounding each nest where I trapped small mammals by summing the total number of captured rodents (i.e., excluding recaptures) for each of the 2 trapping sessions and adding 1 to the total for each session. I added 1 to the total in each session so that I would not have any zeros. I summed the 2 sessions to calculate relative small mammal abundance for both sessions combined. I used paired *t*-tests to compare relative small

mammal abundance between the 2 trapping sessions each year. I used a *t*-test to compare relative small mammal abundance between the 2 study years. I used simple linear regression with each of the 3 measures of relative small mammal abundance (from the first trapping session, the second session, or both sessions combined) to determine which one explained more of the variation in dispersal age. I examined the influence of relative small mammal abundance on dispersal age in 2 ways: 1) without controlling for parental departure and hatch date, and 2) controlling for parental departure and hatch date. I used simple linear regression (when I did not include covariates in the model) and multiple linear regression (when I included covariates) to examine the effects of relative small mammal abundance on dispersal age. The response variable was dispersal age in both regression models, and the explanatory variables for the 2 models were: 1) relative small mammal abundance, and 2) relative small mammal abundance, parental departure, and hatch date.

I also examined the influence of relative small mammal abundance on parental departure in 2 ways: 1) without controlling for hatch date, and 2) controlling for hatch date. I used simple linear regression (when I did not include hatch date in the model) and multiple linear regression (when I included hatch date) to examine the effects of relative small mammal abundance on parental departure. The response variable was parental departure in both regression models, and the explanatory variables for the 2 models were: 1) relative small mammal abundance, and 2) relative small mammal abundance and hatch date.

I used a *t*-test to compare relative flea load between the 2 study years. I examined the influence of relative flea load on dispersal age in 2 ways: 1) without controlling for parental departure and hatch date, and 2) controlling for parental departure and hatch date. I used simple linear regression (when I did not include covariates in the model) and multiple linear regression (when I included covariates) to examine the effects of relative flea load on dispersal age. The response variable was dispersal age in both regression models, and the explanatory variables were: 1) relative flea load, and 2) relative flea load, parental departure, and hatch date.

I also examined the influence of relative flea load on parental departure in 2 ways: 1) without controlling for hatch date, and 2) controlling for hatch date. I used simple linear regression (when I did not include hatch date in the model) and multiple linear regression (when I included hatch date) to examine the effects of relative flea load on parental departure. The response variable was parental departure in both regression models, and the explanatory variables were 1) relative flea load, and 2) relative flea load and hatch date.

I also used multiple linear regression to assess the effects of both relative small mammal abundance and relative flea load on dispersal age together in one model so that I could examine whether there was an interaction between these 2 variables.

RESULTS

Telemetry

Of the 170 radio-collared juveniles, 75 initiated dispersal by roosting >300 m or dying >2 km from their nest (Table 1). I assumed another 28 birds dispersed from the study area after I could not locate them using vehicle and aerial surveys. Another 57 juveniles died <300 m from their nest prior to dispersal. I excluded another 6 juveniles from analyses which were found dead >300 m but <2 km from their nest burrow because I could not determine their dispersal fate. Another 4 juveniles were still present at their nests at the end of the field seasons (5-Oct-2002 and 24-Oct-2003), which I excluded from analyses because they may have over-wintered (i.e., did not disperse until next breeding season). Juvenile owls do occasionally over-winter in this study area (Conway et al. 2003). Therefore, a total of 103 juveniles initiated dispersal (75 juveniles seen roosting >300 m from their nest, and 28 juveniles whose signal could not be found within the study area). Of these 103 juveniles that initiated dispersal, 5 were from 1 nest where I attempted to radio-collar the entire brood simultaneously in 2002. These juveniles dispersed within 5 days of each other, and I averaged their dispersal dates and ages prior to analysis. Another 2 of the 103 juveniles that dispersed were from 1 nest where I mistakenly radio-collared 2 juveniles in 2003. These 2 juveniles departed the natal area at widely different ages (97 and 139 days old), but I nevertheless averaged their dispersal dates and ages prior to analysis. Therefore, of the total 103 juveniles that dispersed, I had a sample size of 98 dispersal ages ($n_{2002} = 47$; $n_{2003} = 51$).

Dispersal age

Mean dispersal age was 73 (95% CI: 68 – 78; range 42 – 154) days old; juveniles dispersed younger (t_{96} = -3.0, P = 0.003) in 2002 (# = 66, 95% CI: 61 – 70 days old) compared to 2003 (# = 80, 95% CI: 72 – 87 days old; Table 2). If I exclude all juveniles that received either food or ectoparasite treatments, mean dispersal age was 76 (95% CI: 67 – 85, range 50 – 136) days old and did not differ from the overall mean of 73 days old (t_{23} = 0.7, P = 0.747). Using dispersal ages of juveniles at untreated nests only, juveniles still initiated dispersal older in 2003 compared to 2002 [$\#_{2002}$ = 69 (95% CI: 55 – 81) days old, $\#_{2003}$ = 84 (95% CI: 72 – 97) days old; t_{22} = -1.8, P = 0.078]. Mean dispersal date among all juveniles for both years combined was 1 Aug (range 22 Jun – 11 Oct), but juveniles dispersed earlier (t_{96} = -2.1, P = 0.036) in 2002 (# = 26 Jul) than in 2003 (# = 6 Aug). Mean hatch date for both years was 20 May (range 29 Apr – 3 Jul), and did not differ between years (t_{96} = 1.2, P = 0.231).

After I controlled for parental departure, juveniles in 2002 dispersed 7.6 (95% CI: -15.9 – 0.6) days younger than in 2003 ($F_{2,94}$ = 22.6, P < 0.0001; year effect t_{94} = 1.8, P = 0.069). After I controlled for parental departure, neither natal dispersal date nor hatch date differed between years (P > 0.242 in both cases).

Covariates

Age of the juvenile on the date that the second of the juvenile's parents departed the natal area explained more variation than the other 3 measures of parental departure (adjusted R^2 = 0.293, t_{95} = 6.4, P < 0.0001; Fig. 4).

Hatch date was more closely associated with dispersal age than parental departure in 2002 (birds that hatched early in the season dispersed at an older age compared to birds that hatched late in the season; $t_{43} = 2.3$, $P = 0.026$; Table 3, Fig. 5). In contrast, parental departure was more important in 2003 ($t_{48} = 4.9$, $P < 0.0001$; Fig. 6).

Therefore, to isolate the effects of food and ectoparasites, I controlled for hatch date and parental departure by using hatch date and age of the radio-collared juvenile on the date the second of its parents departed their natal area as covariates in the analyses.

After controlling for parental departure and hatch date, juvenile females initiated natal dispersal earlier than males each year, but the difference was not statistically significant [$\#_{females} = 71$ (95% CI: 62-79) days old; $\#_{males} = 74$ (95% CI: 67-80) days old; $t_{83} = -0.5$, $P = 0.619$; Table 4].

Food and ectoparasite treatments

After controlling for hatch date and parental departure, juveniles at nests supplemented with food in 2002 initiated dispersal 9.9 days younger (95% CI: -18.3 – -1.5; Fig. 7; Table 5) than juveniles at control nests ($t_{41} = 2.4$, $P = 0.022$). In contrast, juveniles at nests supplemented with food in 2003 initiated dispersal 6.0 days older (95% CI: -6.7 – 18.7) than juveniles at control nests, but the trend was not statistically significant ($t_{46} = 0.9$, $P = 0.345$). I then tested whether food supplements influenced parental departure. After controlling for hatch date, adults at nests that received food supplements in 2002 departed the natal area when their offspring were 5.5 days older (95% CI: -4.6 – 15.6) than adults at control nests, although this trend was not statistically

significant (t_{42} = 1.1, P = 0.276; Table 6). Food supplements did not influence parental departure in 2003 (t_{47} = 0.3, P = 0.744).

After controlling for hatch date and parental departure, juveniles at nests treated for ectoparasites in 2002 initiated dispersal 3.9 days older (95% CI: -4.4 – 12.3; Table 5; Fig. 8) than juveniles at control nests, but this trend was not statistically significant (t_{41} = 0.9, P = 0.348). In contrast, juveniles at nests treated for ectoparasites in 2003 initiated dispersal 14.7 days younger (95% CI: -27.4 – -2.0; t_{46} = 2.3, P = 0.024) than controls. I then tested whether ectoparasite treatments influenced parental departure. Ectoparasite treatments did not influence parental departure (ectoparasite treatment P > 0.313 in all cases; Table 6).

Effectiveness of treatments

Food supplements were effective. Food-supplemented juveniles were heavier in relation to their age than control juveniles (interaction of food treatment × age captured t_{94} = 3.1, P = 0.003, both years combined; Table 7). Based on the small mammal trapping data, I was able to determine that ambient food differed between the 2 study years (see *Relative small mammal abundance* below). In 2002 (the low food year), control juveniles did not gain weight as they aged (Fig. 9). In 2003 (the high food year), both control and supplemented juveniles gained weight as they aged, but supplemented juveniles gained weight at a faster rate. Food supplements did not influence percent wing feather emergence relative to age (interaction of food treatment × age captured t_{42} = 1.1, P = 0.289) in 2002.

The ectoparasite treatments were also effective, although only in 2003. I did not find a difference in relative flea load between juveniles treated for ectoparasites and controls in 2002 (t_{45} = -0.665, P = 0.509; Fig. 10). In 2003, juveniles treated for ectoparasites had lower relative flea loads than controls (flea load index 0.75 vs. 1.31, respectively; t_{49} = 1.9, P = 0.064).

Relative small mammal abundance

Small mammal trapping did not influence dispersal of juveniles. Juveniles at nests where I trapped small mammals did not disperse at a different age than juveniles at nests where I did not trap small mammals (t_{19} = 1.3, P = 0.203).

The mean date of each small mammal trapping session was 2 weeks later in 2002 (4 Jul and 18 Aug) compared to 2003 (20 Jun and 3 Aug). Relative small mammal abundance decreased from the first trapping session to the second trapping session in 2002 (paired *t*-test, t_{33} = -4.4, P < 0.0001; Fig. 11) but not in 2003 (paired *t*-test, t_{15} = 1.6, P = 0.127). Relative small mammal abundance during the second trapping session was more than 2 times higher in 2003 than in 2002 (t_{49} = -3.1, P = 0.003). The index of small mammal abundance from the second trapping session (mid-summer to early fall) explained more variation in dispersal age (t_{35} = 1.7, P = 0.103) than the index from the first trapping session or the index of both trapping sessions combined. Therefore, I used the index from the second trapping session for analyses.

Relative small mammal abundance did not influence dispersal age either year (Table 8; Fig. 12). In 2003, relative small mammal abundance appears to be associated

with older dispersal age, but the effect is due to 1 outlier. If I exclude that juvenile, the association disappears ($t_{10} = 0.3$, $P = 0.709$). I found no association between parental departure and relative small mammal abundance in 2002 ($t_{22} = 1.3$, $P = 0.217$; Table 9; Fig. 13). However, adults at nests with higher relative small mammal abundance departed the natal area when offspring were older in 2003 ($t_{11} = 4.6$, $P = 0.0008$) and when both years are combined ($t_{35} = 5.3$, $P < 0.0001$).

Relative flea load

I failed to detect a difference in relative flea load between 2002 and 2003 ($t_{96} = 1.3$, $P = 0.211$; Fig. 14). Relative flea load did not affect dispersal age (Table 10; Fig. 15) or parental departure (Table 11).

Interactions in the observational study

Relative flea load on juvenile owls was not associated with relative small mammal abundance in the area surrounding the nest burrow in either year or both years combined (pairwise correlation, both years combined, $r = -0.0$, $n = 37$, $P = 0.915$). However, I found an interaction between relative flea load and relative small mammal abundance when examining how both affected dispersal age after I controlled for parental departure. The interaction was significant in 2003 (relative small mammal abundance × relative flea load $t_8 = 8.6$, $P < 0.0001$) but not in 2002 (relative small mammal abundance × relative flea load $t_{19} = 1.1$, $P = 0.291$). Unfortunately, attempts to further explore the meaning of the interaction failed due to small sample size.

DISCUSSION

Variation in dispersal age

Burrowing owls vary widely in dispersal age. The youngest juvenile to initiate dispersal did so in 2002 at 42 days old, whereas the oldest delayed dispersal until 154 days of age in 2003, a 3.7-fold difference (# = 73).

Mean dispersal age differed between study years, with juveniles in 2002 initiating dispersal younger (# = 66) overall than in 2003 (# = 80). Even when I exclude either the 42-day-old disperser or the 154-day-old disperser, or both, mean dispersal age differed between the 2 years. The range of variation also differed between the study years. For example, the oldest juvenile to initiate dispersal in 2002 was 114 days old, as compared to the 154-day-old juvenile in 2003. But the difference in range of variation between the study years was not only due to the oldest juvenile to disperse. In 2002, 75% of all juveniles had initiated dispersal by the time they were 72 days old. In contrast, the age by which 75% of all juveniles had initiated dispersal in 2003 was 97 days old. The difference in range of variation between years is even more pronounced after considering that the youngest juveniles to initiate dispersal each year did not differ very much in age (42 days old in 2002 and 46 days old in 2003).

Juvenile burrowing owls in Idaho initiated dispersal younger (# = 57.6 ± 3.4 days old; range 31 – 77 days; King 1996) than those in my study in Washington. The difference in dispersal ages between the 2 studies may indicate that food at the end of summer was lower in Idaho during the years of that study than in Washington during my study. Juvenile burrowing owls in Saskatchewan initiated dispersal at 50.0 ± 1.3 days old

(range 28 – 65 days; Todd 2001b). However, the definition of dispersal in the Saskatchewan study was broad, encompassing any movements made after fledging regardless of distance or time away from the nest. Other data presented in that study suggested that some of these juveniles first moved ≥300 m from the nest at about 60-100 days old, which resembled my results.

Among other species, relatively few studies have examined variation in dispersal age, yet variation in dispersal age seems common. Often, researchers reported the number of days from fledging to dispersal, but did not provide age at dispersal. Although these studies were not necessarily examining variation in dispersal timing, reporting dispersal timing as the number of days from fledging (or independence) until dispersal may be problematic when examining variation in dispersal timing or age because the cause for the variation may act on the period prior to fledging (or independence). Hence, true variation in dispersal timing may not be apparent if one controls for fledging (or independence) date. Other studies only provided mean dispersal age, not range. Nevertheless, the following are a sample of the range of variation in dispersal timing (i.e., age or number of days after fledging) across a variety of bird species. Great bustards (*Otis tarda*) in Spain varied in dispersal age from 6-15 months (Alonso et al. 1998). Goshawks (*Accipiter gentilis*) in Gotland, Sweden initiated natal dispersal between 65-95 days of age (Kenward et al. 1993). Spanish imperial eagles (*Aquila adalberti)* initiated natal dispersal from 116-162 days old (Ferrer 1993). Mexican spotted owls (*Strix occidentalis lucida*) in Arizona initiated dispersal 73-125 days after fledging (Ganey et al. 1998). Eastern screech owls (*Otus asio*) initiated dispersal 45-65 days after fledging

(Belthoff and Ritchison 1989). Some spruce grouse (*Falcipennis canadensis*) in Canada initiated natal dispersal in autumn, whereas others delayed dispersing until the following spring (Keppie 2004). Hence, burrowing owls are not unusual in their average dispersal age, but do seem to be among the species that have wider ranges of variation in dispersal age. However, relatively few studies have focused on variation in dispersal age.

Food and ectoparasites influence dispersal age

My study provides evidence that both food and ectoparasites influence dispersal age, independently of parental departure and hatch date. Additionally, I showed that ambient food influenced parental departure, and that hatch date and parental departure influenced dispersal age. Food supplements caused juveniles to disperse younger in the lower food year (2002), but had no effect in the higher food year (2003). In contrast, ectoparasite treatments had no effect in the low food year when juveniles were presumably food-stressed as indicated by unsupplemented juveniles not gaining weight with age that year. In the high food year, ectoparasites appeared to be important because juveniles not treated for ectoparasites initiated natal dispersal later than controls.

Food

The effects of food on dispersal age are context-dependent. My data suggest that when ambient food is lower, juveniles that grow faster will disperse younger. However, when food is abundant, juveniles that grow faster do not differ in dispersal age compared to those that grow slower. The latter situation suggests that if food is sufficiently

abundant, juveniles are under no pressure to disperse quickly. Parents may be more tolerant of juvenile presence during years when food is abundant.

Amount of ambient food available to owls differed between the 2 study years, but only during the second small mammal trapping session in late summer. Index of small mammal abundance for the first trapping sessions in early summer did not differ between the 2 years. Dispersal age also differed between the 2 study years, indicating that the decision to initiate natal dispersal may have been based on food available in late summer, when juveniles approached independence.

In 2002, parental departure was not associated with dispersal age, but hatch date was. In that same year, supplemented juveniles grew faster and initiated dispersal younger than controls although their parents departed the natal area when their offspring were older than control offspring. Hence, in low-food years, parents may be less tolerant of allowing offspring to remain in the natal area or offspring may initiate dispersal independent of parents. Previous authors have not reported instances of aggression between parents and offspring or among offspring in burrowing owls (Haug et al. 1993, King 1996), but I saw instances of aggression among offspring in very late summer and early fall (pers. obs.). Hence, burrowing owl parents and offspring may not have cause to be aggressive toward each other in higher food years or until late in the season when food is more scarce.

Food-supplemented juvenile burrowing owls in Saskatchewan did not disperse at a different age than unsupplemented juveniles (Todd 2001b). In that study, however, food supplements stopped after juveniles reached fledging age (41 days), and dispersal

was defined differently than in my study. Hence, the results of the 2 studies are not directly comparable. Juvenile burrowing owls in Idaho that were supplemented with food dispersed later than controls (King 1996). This is opposite of the pattern I found in 2002. However, all the juveniles in the Idaho study were aged based on morphometric measurements, whereas I aged juveniles based on partial clutch sizes and breeding cycle phenology. Given that supplemented juveniles weighed more and grew faster than controls (King 1996), age estimates of supplemented juveniles may have been overestimated relative to controls in the Idaho study. Additionally, my sample sizes were larger than those in the Idaho study (n = 98 and 25, respectively).

Even if supplemented juveniles initiated dispersal later than controls in Idaho, control juveniles in that study had faster flight feather growth compared to supplemented juveniles. The author suggested that the accelerated feather growth might have been caused by food stress. The reasoning was that control (food-stressed) juveniles allocated more resources to feather growth as opposed to somatic growth so that they could initiate dispersal sooner. Conversely, supplemented juveniles allocated more resources to somatic growth because they had sufficient food in the natal area to allow them to remain there. Juvenile goshawks in Gotland, Sweden sometimes initiated dispersal as soon as their flight feathers were grown, but some responded to supplemental feeding by delaying dispersal (Kenward et al. 1993). Completion of flight feather growth has been considered a proximate cue for dispersal or nest departure (Kenward et al. 1993, Deguchi et al. 2004), allowing some juveniles to disperse but not necessarily prompting dispersal in all juveniles. In my study, emergence of flight feathers was not influenced by food

supplements in 2002 (low food year), but supplemented juveniles did gain weight faster than controls and were able to disperse sooner. Perhaps in this low food year, all juveniles were food-stressed and allocated resources to feather growth, but supplemented juveniles were able to achieve a second threshold (such as weight gain) earlier, and hence dispersed earlier.

Juveniles of other species have reacted differently to food supplements, higher relative small mammal abundance, or better physical condition. In some species, supplemented juveniles, juveniles in areas with higher food abundance, or juveniles in better condition dispersed sooner or younger (Nilsson and Smith 1985, Ferrer 1992, Ellsworth 1997, Takahashi et al. 1999, Willey and van Riper III 2000, Mínguez et al. 2001). In contrast, higher food abundance or food supplements have resulted in later or older dispersal in other species (Walker 1988, Kenward et al. 1993, Bustamante 1994, Frumkin 1994, Kennedy and Ward 1994, King 1996, Gjerdrum 2004). In other studies, food supplements had no effect on dispersal timing (Bustamante 1994, Redpath et al. 2001, Todd 2001b). Some of the differences in results are probably due to different methods and definitions of dispersal, but responses to supplemental feeding or high ambient food also likely vary across species and local conditions. In my own study, response to supplemental feeding varied by year despite use of the same methods each year.

Parents of some species responded to food supplements by decreasing the amount of food they provided their young (Bolton 1995, Cook and Hamer 1997, Hamer et al. 1998, Wernham and Bryant 1998, Redpath et al. 2001, Harding et al. 2002, Gjerdrum

2004). In such cases, supplemented juveniles received the same or only slightly more food than control juveniles (Bolton 1995, Cook and Hamer 1997, Hamer et al. 1998). However, measures of body condition (e.g., mass, wing length, tarsus length) are often better for supplemented juveniles (Bolton 1995, Wernham and Bryant 1998, Harding et al. 2002, Gjerdrum 2004), indicating that parents may be reducing provisioning in response to juveniles' decreased needs, not in response to the food supplements themselves. I did not examine parental provisioning rates, but if burrowing owl parents reduce provisioning at supplemented nests, juveniles at supplemented and control nests may be receiving equal amounts of food, especially when food is scarce (as in 2002). However, in both years of my study, supplemented juveniles gained weight faster than control juveniles. Despite this, reduced parental provisioning may itself be a proximate cue for dispersal, and thus supplemented juveniles dispersed sooner than controls in the low food year.

Ectoparasites

In the year that food was relatively abundant (2003), juveniles treated for ectoparasites had slightly lower relative flea loads and initiated dispersal younger than controls. One explanation for why juveniles treated with diatomaceous earth dispersed younger than controls in 2003 could be that the treatment had a negative effect on the juveniles. However, my data do not support that explanation because juveniles treated for ectoparasites in 2002 dispersed slightly later than controls. Unfortunately, my measure of ectoparasite load was coarse and did not include many ectoparasites that were

more difficult to see than fleas. Nevertheless, the proven efficacy of diatomaceous earth (Dawson 2004), coupled with the fact that the diatomaceous earth treatment reduced fleas (in 2003) and had an effect on dispersal age (in 2003) suggests that ectoparasites play a significant role in burrowing owl dispersal decisions, especially in the absence of food-stress.

To my knowledge, no other studies have examined the role of ectoparasites on natal dispersal in burrowing owls. Indeed, few studies have examined the effect of ectoparasites on natal dispersal (especially dispersal timing) in any species (Boulinier et al. 2001). However, cliff swallows (*Hirundo pyrrhonata*) at sites heavily infested with ectoparasites departed the natal colony earlier in the nesting cycle than swallows at less-infected sites (Loye and Carroll 1991). On the other hand, great tit (*Parus major*) nestlings experimentally infested with ectoparasites had a prolonged nestling period (Fitze 2004), reduced body mass and size, increased begging, and caused male parents to increase the frequency of their feeding trips (Christe et al. 1996). Hence, nestling development occurred over an extended period, causing tits to depart the nest later. In my study in 2003, juvenile burrowing owls at nests treated with diatomaceous earth (who therefore should have fewer ectoparasites) dispersed younger, and the observational data suggests that juveniles with lower flea loads also may have dispersed younger. Juvenile burrowing owls with higher ectoparasite abundances may also develop slower, resulting in later dispersal. Unfortunately, I do not have data to test this prediction.

Some of the fleas found on burrowing owls in Idaho have been identified as rodent fleas (Smith and Belthoff 2001) and were probably brought into the burrow with

prey items. Thus, high relative flea load may not indicate that a juvenile is less healthy, but may simply reflect some other factor such as increased caching of prey. I found no relationship between relative small mammal abundance and relative flea load, but the significant interaction between relative small mammal and relative fleas indicates that the two affect dispersal age in a complex manner.

Use of multiple approaches

The results and approaches used in my study raise important conceptual issues regarding hypothesis testing and ecological methodology. The flaws and benefits of experimental versus observational approaches to hypothesis testing have been discussed previously (Romesburg 1981, Eberhardt and Thomas 1991, Milinski 1997). If I had relied solely on an experimental approach, I would not have been able to explain why food affected dispersal age 1 year but not the other. If I had relied solely on an observational approach, I would have concluded that food does not directly influence dispersal age. However, my study suggests that the answer is context-dependent, and intrinsic factors that influence dispersal age (such as parental departure) may be influenced by food without food directly influencing dispersal age. Therefore, although my own and other studies yielded significant results under a given approach in a given year, the effects of food and ectoparasites on dispersal age seemed to vary according to changing selection regimes.

In one year of my study, one process (food) influenced dispersal behavior, and in another year a second process (parasitism) influenced the same behavior. Additionally,

based on previous research, I could have made predictions in either direction about how each process would influence the behavior. As researchers, we strive to frame ecological questions in the context of hypothesis testing because that is the most reliable method we have for discovering knowledge in an unbiased manner. Unfortunately, hypothesis testing, especially in short-term studies, often leads to results in which we show an effect one year, but not another. In my own study, experimental data show that when food is low, food matters. When food is not low, ectoparasites matter. Changing conditions lead to conclusions in which one hypothesis is supported and another rejected, and yet the opposite may be found the following year.

My study indicates that although an experimental approach allows for control of intrinsic and ambient factors, incorporating observational data is valuable to the interpretation of the results. Experimental supplements during years when the resource being manipulated is already higher than normal may not show an effect, yet that resource may still directly influence the behavior of interest. Hence, we need to document ambient conditions that may influence selection regimes of animals so that responses to experimental manipulations can be put into context. Additionally, experimental studies conducted in >1 year reduces the likelihood that results are masked or confounded by ambient conditions in a single year.

Experimental manipulations have their own set of confounding issues. For example, we manipulate conditions (e.g., food, ectoparasites, temperature) for animals, and measure their response (e.g., body mass, growth, feather emergence, morphometric measurements). However, these responses cannot always then be used to assign values to

the response variable in question. In my study, supplemental feeding caused juveniles to gain weight faster. If I used body mass or other measurements of development to gauge juvenile age as has been done in other studies (King 1996, Mínguez et al. 2001), I would have surely found that supplemented juveniles dispersed older even if all juveniles had dispersed at the same age. Additionally, because ambient conditions vary, some manipulations (e.g., supplementing food) may not be effective in some years (e.g., high-food years), potentially leading to inappropriate conclusions.

Future studies should incorporate manipulations in both directions (i.e., also removing food and increasing ectoparasites) to strengthen conclusions. Additionally, measuring ambient food or other factors should be done on a larger scale. Burrowing owls will forage near their nest burrow, but will also forage far from their nest (Thompson and Anderson 1988). Therefore, measuring relative small mammal abundance immediately around nest burrows may not provide a meaningful index of how much food is available to a particular family group.

Other ultimate factors may also influence dispersal age. For example, other burrows near the natal burrow are frequently used by juveniles before dispersal and have been shown to be an important feature in nest-site selection (Plumpton 1992, Lantz 2005) and possibly juvenile predator avoidance (King and Belthoff 2001). Also, juvenile owls are frequently killed by predators (36% of all documented juvenile mortalities in 2003 were due to predation; Conway et al. 2003) and risk of depredation may influence dispersal age. Future studies should test how predation and the presence and type of refugia or shelter near the nest influence dispersal age.

MANAGEMENT IMPLICATIONS

Burrowing owls are decreasing over much of their northern range (Klute et al. 2003). In Saskatchewan, nests that were supplemented with food fledged more offspring (Wellicome 2000), but the population continued to decrease even after 7 years of supplemental feeding (Todd 2001b). Supplemented juveniles had higher probability of post-fledging mortality compared to unsupplemented juveniles in Saskatchewan (Todd 2001b). In my study, supplemented juveniles dispersed younger than controls, but the effects of younger dispersal are unknown. Sample sizes of recruited juveniles in my study area were small, but juvenile male white-crowned sparrows (*Zonotrichia leucophrys oriantha*) were more likely to be recruited into the breeding population the longer they remained in that population as juveniles (Morton et al. 1991). Hence, supplemental feeding does not appear to be a viable strategy to encourage burrowing owl juveniles to remain in the natal area or to increase local recruitment or local population size.

In my study, higher relative small mammal abundance was associated with later parental departure, and natal dispersal was closely and positively correlated with parental departure in the high-food year. In eastern Washington, most burrowing owls nest near or adjacent to agricultural fields. The type of crop and the height of plants might directly affect how much prey is available to burrowing owls. Hence, crops that attract rodents, such as cultivated grains, soybeans, and corn (Fergus 2004), may provide a stable prey source that would allow owls to remain in the natal area if the crops or stubble are present in late summer and early fall. If remaining in the natal area longer is beneficial to adult

or juvenile owls, then areas near owl burrows (such as the corners of crop circles) could be planted with some of these crops to increase local burrowing owl populations.

Juveniles at nests with higher relative flea load dispersed older and treating nests for ectoparasites caused juveniles to disperse younger. In birds, higher ectoparasite abundances have resulted in or been associated with lower local recruitment (Brown and Brown 1992, Allander 1998, Fitze 2004), lower daily survival probability in colonial nesters (Brown and Brown 1986, Brown and Brown 2004), and decreased nest reuse across years (Brown and Brown 1986). Burrowing owls in areas with less human influence have much fewer fleas than owls in our study area (C. Conway, unpubl. data). Hence, treating nests for ectoparasites in areas of high human impact or where juveniles depend heavily on prey items that are prone to fleas may be a viable strategy for increasing local recruitment.

Disruptive activities around nest burrows should be restricted until juveniles depart, not only until they fledge. Juveniles in eastern Washington dispersed at an average age of 73 days old. Juvenile burrowing owls in Idaho dispersed at an average age of 58 days old (King 1996). In both cases, average dispersal date was in late July, and late-summer dispersal appears to be common in many burrowing owl populations (King 1996). Therefore, disruptive activities around the nest should be limited until at least late summer, but preferably until juveniles are at least 73 days old or until they disperse from the natal area.

Table 1. Fate of radio-collared juvenile burrowing owls in eastern Washington, 2002 and 2003. Juveniles that initiated natal dispersal were 1) seen roosting >300 m from their nest burrow on >1 visit, or 2) found dead >2 km from their nest. Juveniles whose signal could not be re-located within the study area after their signal could no longer be detected in their natal area were also assumed to have initiated dispersal. Juveniles who died before dispersal were found dead <300 m from their nest burrow. Unknown juveniles were found dead >300 m but <2 km from their nest burrow. Juveniles still present at the end of the season had not dispersed by the end of the field seasons (5-Oct-2002 and 24-Oct-2003).

Year	Initiated dispersal	Lost signal (assume dispersed)	Died before dispersal	Unknown	Still present at end of season	Total
2002	38 (43.7%)	13 (14.9%)	31 (35.6%)	2 (2.3%)	3 (3.4%)	87 (100%)
2003	37 (44.6%)	15 (18.1%)	26 (31.3%)	4 (4.8%)	1 (1.2%)	83 (100%)
Total	75 (44.1%)	28 (16.5%)	57 (33.5%)	6 (3.5%)	4 (2.4%)	170 (100%)

Table 2. Mean dispersal age (in days), natal dispersal date, and hatch date of radio-collared juvenile burrowing owls in eastern Washington, 2002 and 2003.

Year	*n*	Mean dispersal age (and range)	Mean dispersal date (and range)	Mean hatch date (and range)
2002	47	65.7 (41.5 – 113.5)	26 Jul (5 Jul – 22 Sep)	21 May (3 May –18 Jun)
2003	51	79.5 (46.0 – 153.5)	6 Aug (22 Jun – 11 Oct)	18 May (29 Apr – 3 Jul)
Total	98	72.9	1 Aug	20 May

Table 3: Influence of hatch date and parental departure (age of radio-collared juvenile on date the second of its parents departed their natal area) on dispersal age of radio-collared juveniles in eastern Washington, 2002 and 2003, when both hatch date and parental departure are in the model. See Figs. 5 & 6.

Year		df	*F*	*P*
2002	Whole Model	2, 43	5.3	0.008
	Hatch date		5.3	0.026
	Parental departure		1.5	0.228
2003	Whole Model	2, 48	12.2	<0.0001
	Hatch date		0.4	0.531
	Parental departure		24.4	<0.0001
Total	Whole Model	2, 94	20.2	<0.0001
	Hatch date		0.05	0.817
	Parental departure		38.2	<0.0001

Table 4: Comparison of dispersal ages (in days) for male and female radio-collared juvenile burrowing owls in eastern Washington, 2002 and 2003.

	females			males				
Year	*n*	#	95% CI	*n*	#	95% CI	*t*	*P*
2002	11	61.6	52.2 – 71.0	35	67.6	62.3 – 72.9	1.1	0.269
2003	19	76.1	62.6 – 89.6	20	83.7	70.5 – 96.9	0.9	0.418
Total	30	70.8	62.2 – 79.4	55	73.5	67.1 – 79.8	0.5	0.619

Table 5: Difference in dispersal age (in days) of radio-collared juvenile burrowing owls at nests that were supplemented with food and treated for ectoparasites compared to controls in eastern Washington, 2002 and 2003. Six models are presented: 3 that include parental departure and hatch date as covariates, and 3 that do not include these covariates.

		With covariates (parental departure and hatch date)					Without covariates				
Year		Age difference	95% CI	df	*F*	*P*	Age difference	95% CI	df	*F*	*P*
2002	Whole Model			4, 41	4.6	0.004			2, 44	2.2	0.126
	Food-supplemented	9.9 d younger	-18.3 – -1.5		5.6	0.022	8.6 d younger	-17.6 – 0.49		3.6	0.063
	Ectoparasite-treated	3.9 d older	-4.4 – 12.3		0.9	0.348	4.0 d older	-5.1 – 13.0		0.8	0.381
2003	Whole Model			4, 46	8.4	<0.0001			2, 48	1.5	0.226
	Food-supplemented	6.0 d older	-6.7 – 18.7		0.9	0.345	7.9 d older	-7.8 – 23.6		1.0	0.318
	Ectoparasite-treated	14.7 d younger	-27.4 – -2.0		5.4	0.024	10.5 d younger	-26.1 – 5.1		1.8	0.183
Total	Whole Model			4, 92	10.9	<0.0001			2, 95	0.5	0.584
	Food-supplemented	0.7 d younger	-8.8 – 7.4		0.0	0.864	1.8 d older	-7.7 – 11.4		0.1	0.707
	Ectoparasite-treated	7.0 d younger	-15.2 – 1.2		2.9	0.092	4.6 d younger	-14.2 – 5.0		0.9	0.342

Table 6: Difference in parental departure (age, in days, of radio-collared juvenile on date the second of its parents departed their natal area) of adult burrowing owls at nests that were supplemented with food and treated for ectoparasites compared to controls in eastern Washington, 2002 and 2003. Six models are presented: 3 that include hatch date as a covariate, and 3 that do not include this covariate.

		With covariate (hatch date)					Without covariate				
Year		Age difference	95% CI	df	*F*	*P*	Age difference	95% CI	df	*F*	*P*
2002	Whole Model			3, 42	3.3	0.029			2, 43	0.8	0.467
	Food-supplemented	5.5 d older	-4.6 – 15.6		1.2	0.276	5.6 d older	-5.3 – 16.5		1.1	0.305
	Ectoparasite-treated	4.1 d older	-6.0 – 14.1		0.7	0.419	3.5 d older	-7.4 – 14.3		0.4	0.525
2003	Whole Model			3, 47	0.4	0.777			2, 48	0.3	0.757
	Food-supplemented	2.8 d older	-14.5 – 20.2		0.1	0.744	2.0 d older	-15.1 – 19.1		0.1	0.818
	Ectoparasite-treated	7.0 d older	-10.3 – 24.2		0.7	0.420	6.1 d older	-10.8 – 23.1		0.5	0.470
Total	Whole Model			3, 93	2.1	0.103			2, 94	0.8	0.445
	Food-supplemented	5.9 d older	-4.2 – 16.0		1.4	0.247	5.3 d older	-5.0 – 15.6		1.0	0.310
	Ectoparasite-treated	5.2 d older	-5.0 – 15.3		1.0	0.313	4.1 d older	-6.2 – 14.4		0.6	0.427

Table 7. Influence of food treatments (food supplemented juveniles compared to controls) on the relationship between body mass and age of radio-collared juvenile burrowing owls in eastern Washington, 2002 and 2003. See Fig. 9.

Year		df	*F*	*P*
2002	Whole Model	3, 43	1.1	0.363
	Food treatment		0.0	0.955
	Age captured		2.3	0.136
	Food treatment × Age captured		2.5	0.118
2003	Whole Model	3, 47	7.3	0.0004
	Food treatment		4.3	0.043
	Age captured		19.7	<0.0001
	Food treatment × Age captured		6.5	0.014
Total	Whole Model	3, 94	6.5	0.0005
	Food treatment		17.3	<0.0001
	Age captured		2.0	0.165
	Food treatment × Age captured		9.6	0.003

Table 8: Influence of relative small mammal abundance on dispersal age of juvenile burrowing owls in eastern Washington, 2002 and 2003. Six models are presented: 3 that include parental departure and hatch date as covariates, and 3 that do not include these covariates.

		With covariates (parental departure and hatch date)			Without covariates		
Year		df	*F*	*P*	df	*t*	*P*
2002	Whole Model	3, 20	0.5	0.671			
	Influence of food abundance		0.0	0.953	22	0.3	0.774
2003	Whole Model	3, 9	1.6	0.247			
	Influence of food abundance		0.0	0.976	11	1.9	0.079
Total	Whole Model	3, 33	1.7	0.187			
	Influence of food abundance		0.0	0.774	35	1.7	0.103

Table 9: Influence of relative small mammal abundance on parental departure (age of radio-collared juvenile on date the second of its parents departed their natal area) of adult burrowing owls in eastern Washington, 2002 and 2003. Six models are presented: 3 that include hatch date as a covariate, and 3 that do not include this covariate.

		With covariate (hatch date)			Without covariate		
Year		df	*F*	*P*	df	*t*	*P*
2002	Whole Model	2, 21	3.0	0.073			
	Influence of food abundance		0.3	0.561	22	1.3	0.217
2003	Whole Model	2, 10	21.5	0.0002			
	Influence of food abundance		29.8	<0.0003	11	4.6	0.0008
Total	Whole Model	2, 34	20.6	<0.0001			
	Influence of food abundance		24.0	<0.0001	35	5.3	<0.0001

Table 10: Influence of relative flea load on dispersal age of juvenile burrowing owls in eastern Washington, 2002 and 2003. Six models are presented: 3 that include parental departure and hatch date as covariates, and 3 that do not include these covariates.

		With covariates (parental departure and hatch date)			Without covariates		
Year		df	*F*	*P*	df	*t*	*P*
2002	Whole Model	3, 42	3.7	0.020			
	Influence of flea load		0.4	0.525	45	0.6	0.553
2003	Whole Model	3, 47	9.0	<0.0001			
	Influence of flea load		2.0	0.161	49	1.6	0.115
Total	Whole Model	3, 93	13.3	<0.0001			
	Influence of flea load		0.0	0.904	96	0.4	0.641

Table 11: Influence of relative flea load on parental departure (age of radio-collared juvenile on date the second of its parents departed their natal area) of adult burrowing owls in eastern Washington, 2002 and 2003. Six models are presented: 3 that include hatch date as a covariate, and 3 that do not include this covariate.

		With covariate (hatch date)			Without covariate		
Year		df	*F*	*P*	df	*t*	*P*
2002	Whole Model	2, 43	4.2	0.021			
	Influence of flea load		0.5	0.479	44	0.5	0.614
2003	Whole Model	2, 48	0.5	0.605			
	Influence of flea load		0.6	0.431	49	0.9	0.375
Total	Whole Model	2, 94	2.1	0.125			
	Influence of flea load		0.3	0.615	95	0.5	0.563

Figure 1. Map of study area with burrowing owl nest locations. The study area was in Grant and Adams counties in eastern Washington.

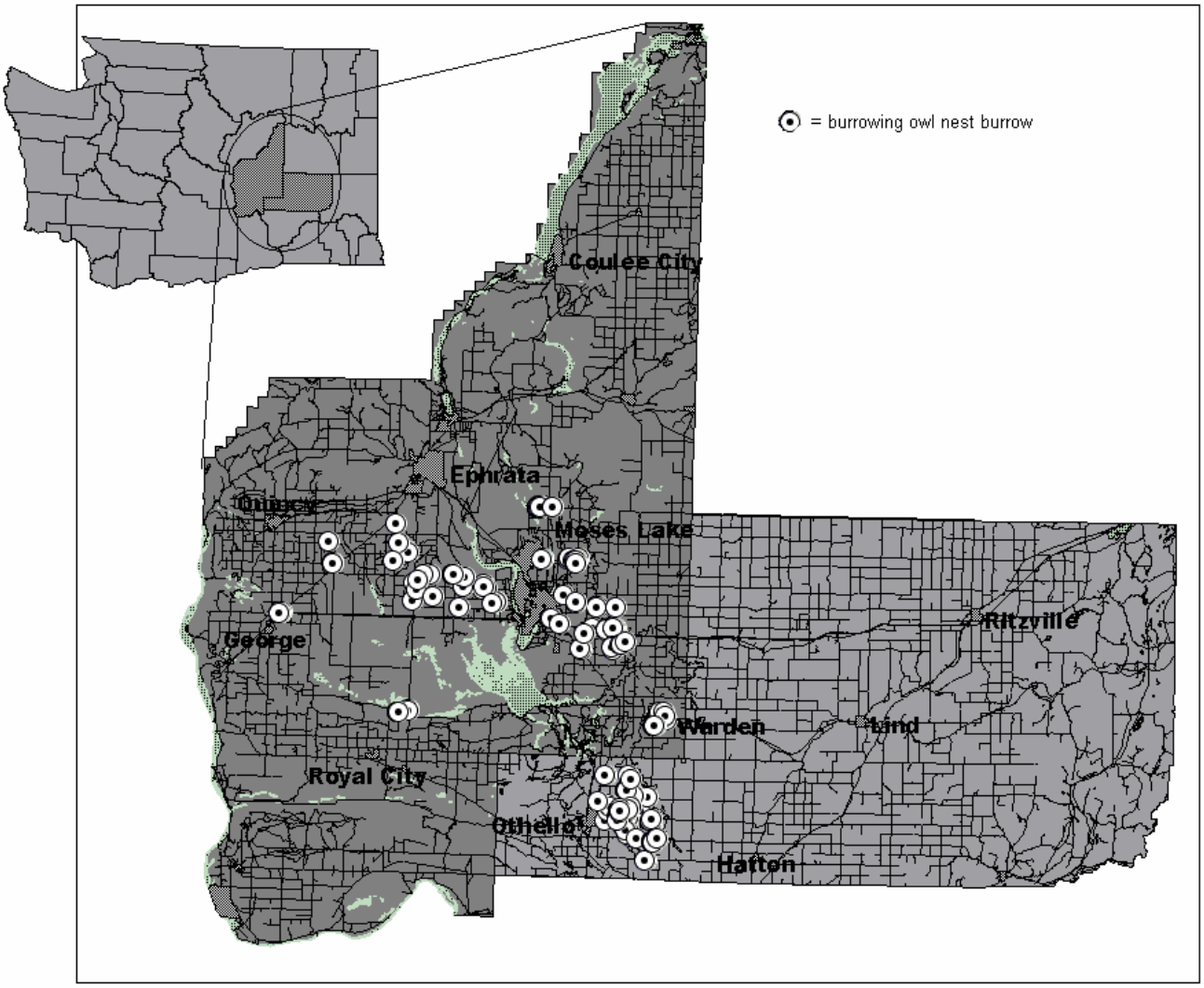


Figure 2. Layout of a typical 8x8 small mammal trapping grid overlaying a burrowing owl nest in eastern Washington in 2002 and 2003 (□ = small mammal trap, ◙ = burrowing owl nest).

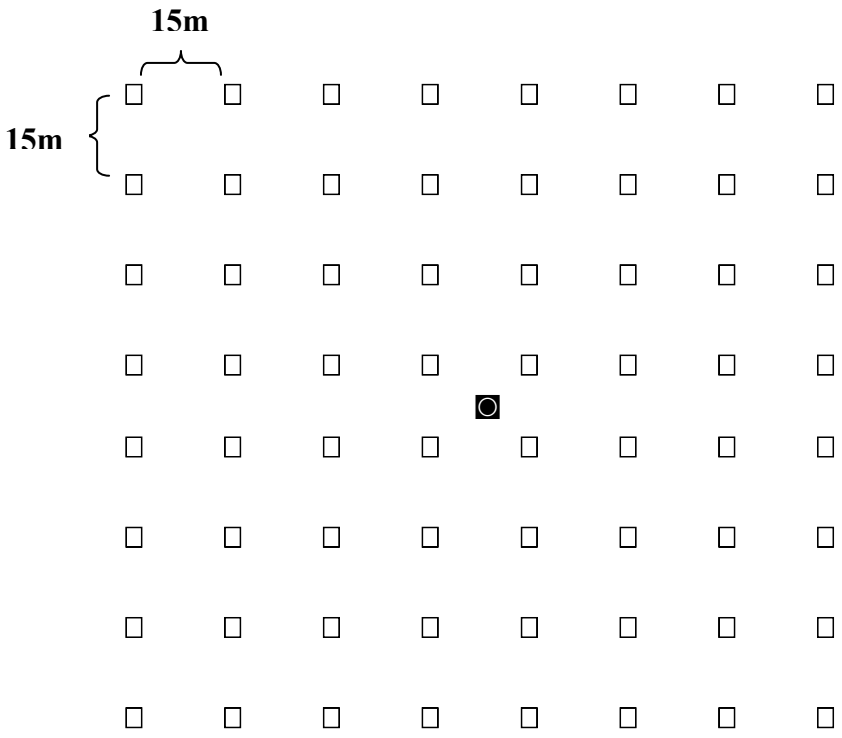


Figure 3. Correlation between relative small mammal abundance (1+ number of small mammals captured) during the first trapping session (4 Jul 2002 and 20 Jun 2003) and the second trapping session (18 Aug 2002 and 3 Aug 2003) in eastern Washington (pairwise correlation, $r = 0.478$, $n = 50$, $P = 0.0004$).

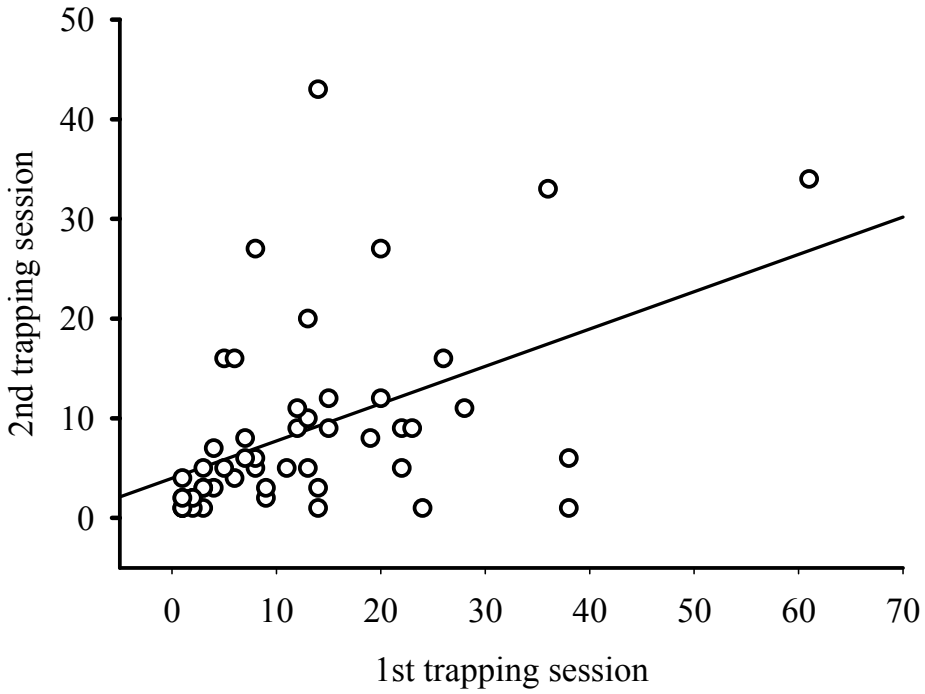


Figure 4. Relationship between dispersal age (in days) and parental departure (age of radio-collared juvenile on date the second of its parents departed their natal area) of burrowing owls in eastern Washington in 2002 and 2003 (adjusted $R^2 = 0.293$, $P < 0.0001$).

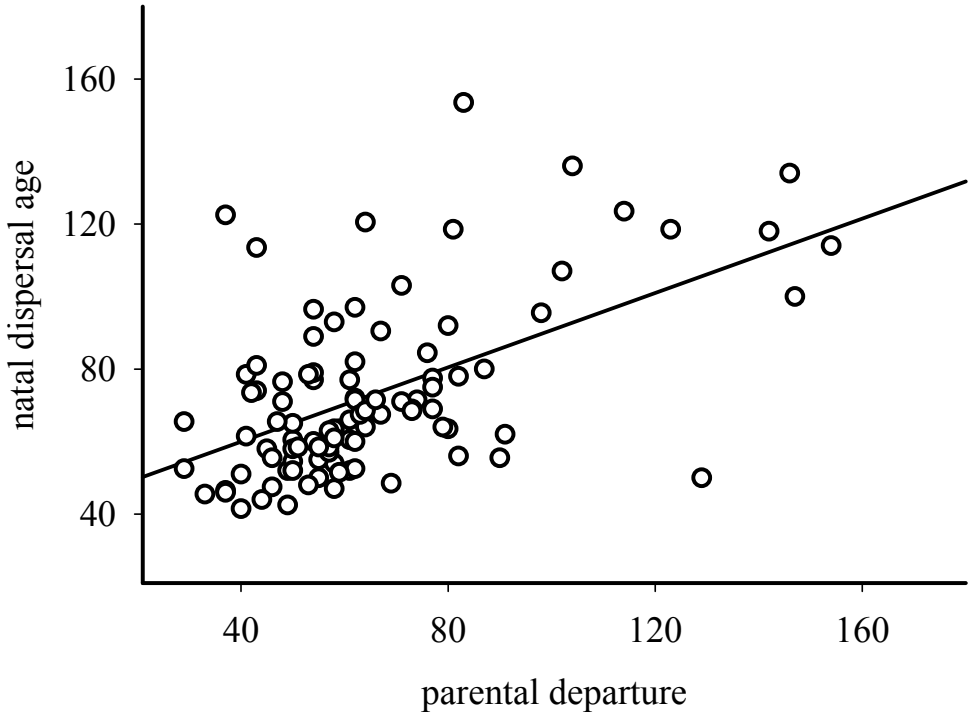


Figure 5. Influence (by year) of hatch date, after controlling for parental departure (age of radio-collared juvenile on date the second of its parents departed their natal area), on dispersal age of radio-collared juvenile burrowing owls in eastern Washington in 2002 ($P = 0.026$) and 2003 ($P = 0.531$).

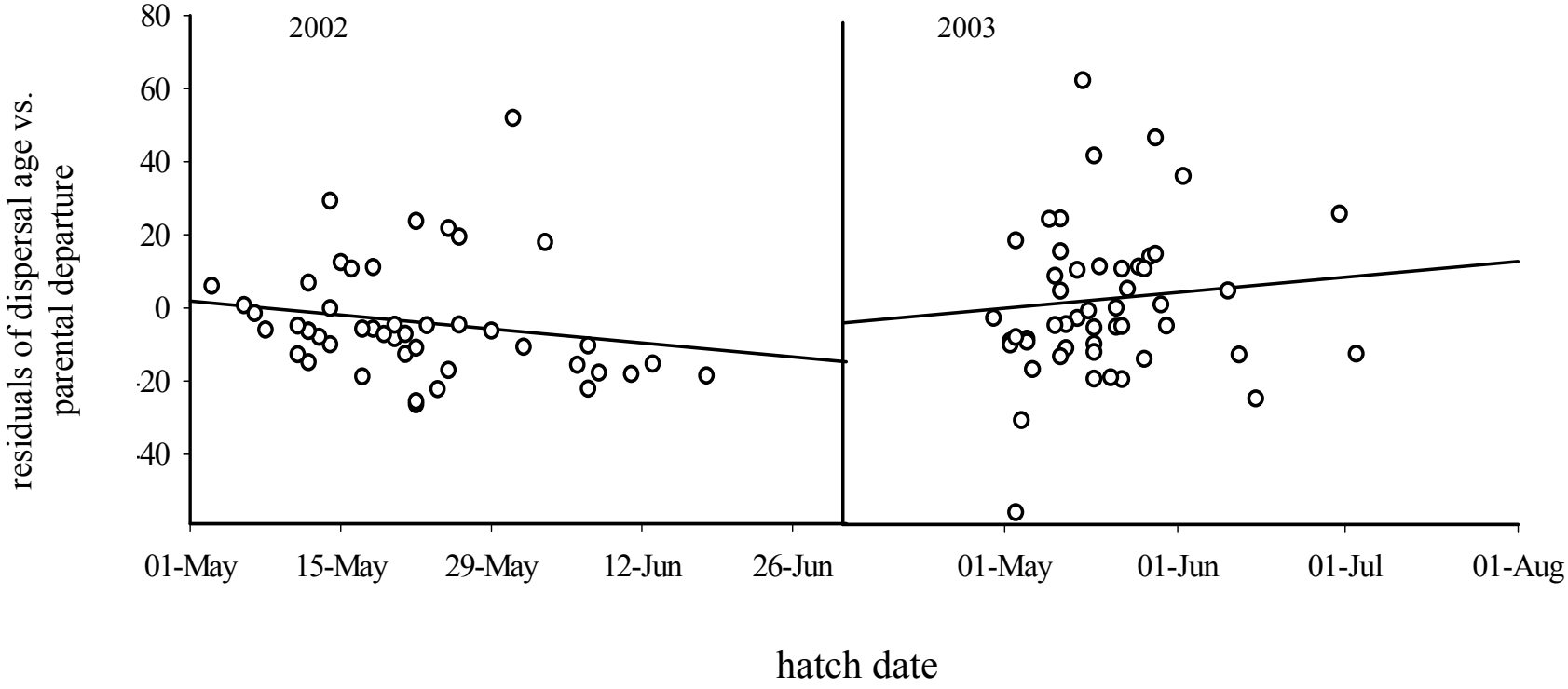


Figure 6. Influence (by year) of parental departure (age of radio-collared juvenile on date the second of its parents departed their natal area), after controlling for hatch date, on dispersal age of radio-collared juvenile burrowing owls in eastern Washington in 2002 ($P = 0.228$) and 2003 ($P < 0.0001$).

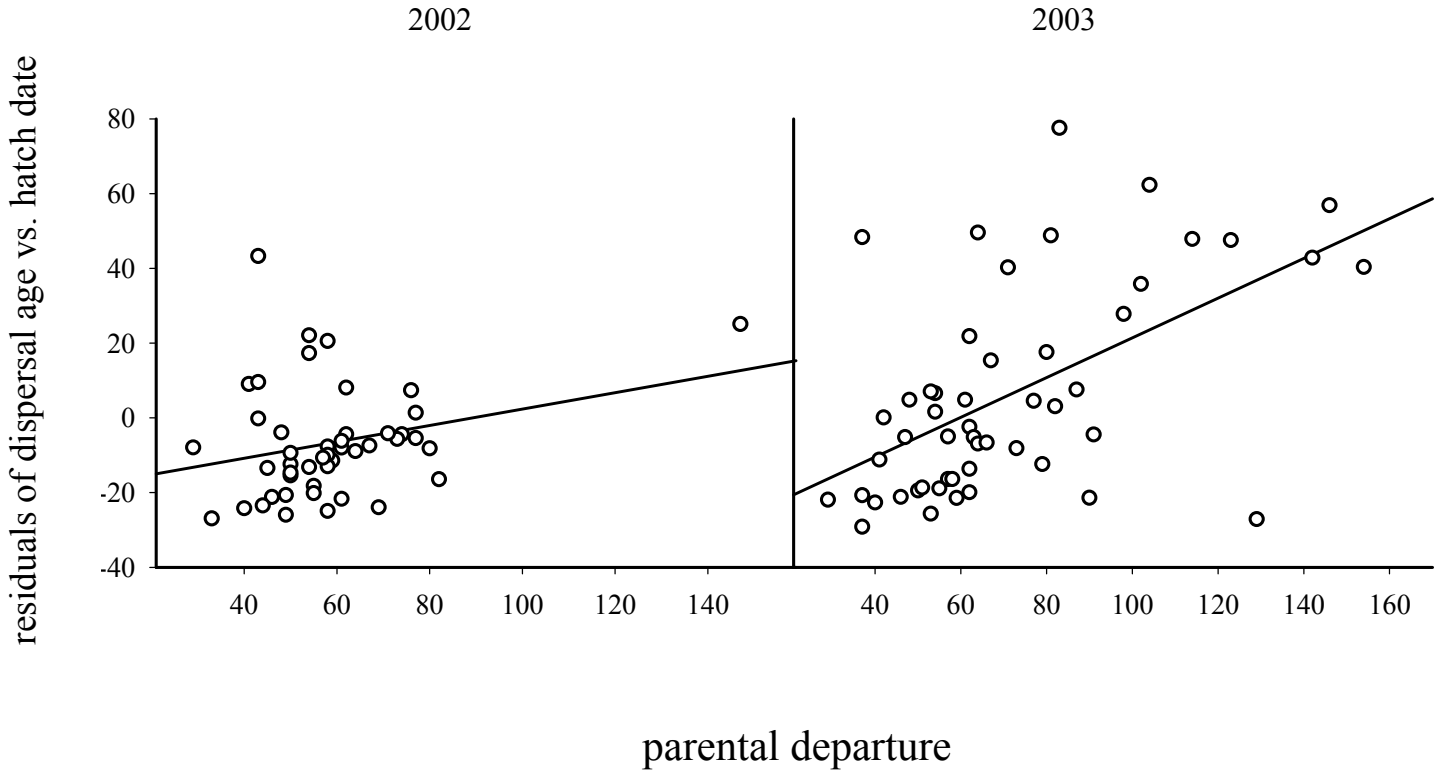


Figure 7: Least squares mean ages (days; ±1 SE) after controlling for hatch date and parental departure (age of radio-collared juvenile on date the second of its parents departed their natal area) that radio-collared juvenile burrowing owls initiated natal dispersal at nests that were repeatedly supplemented with laboratory mice (food) and at control nests (control) in eastern Washington in 2002 ($P = 0.022$) and 2003 ($P = 0.345$).

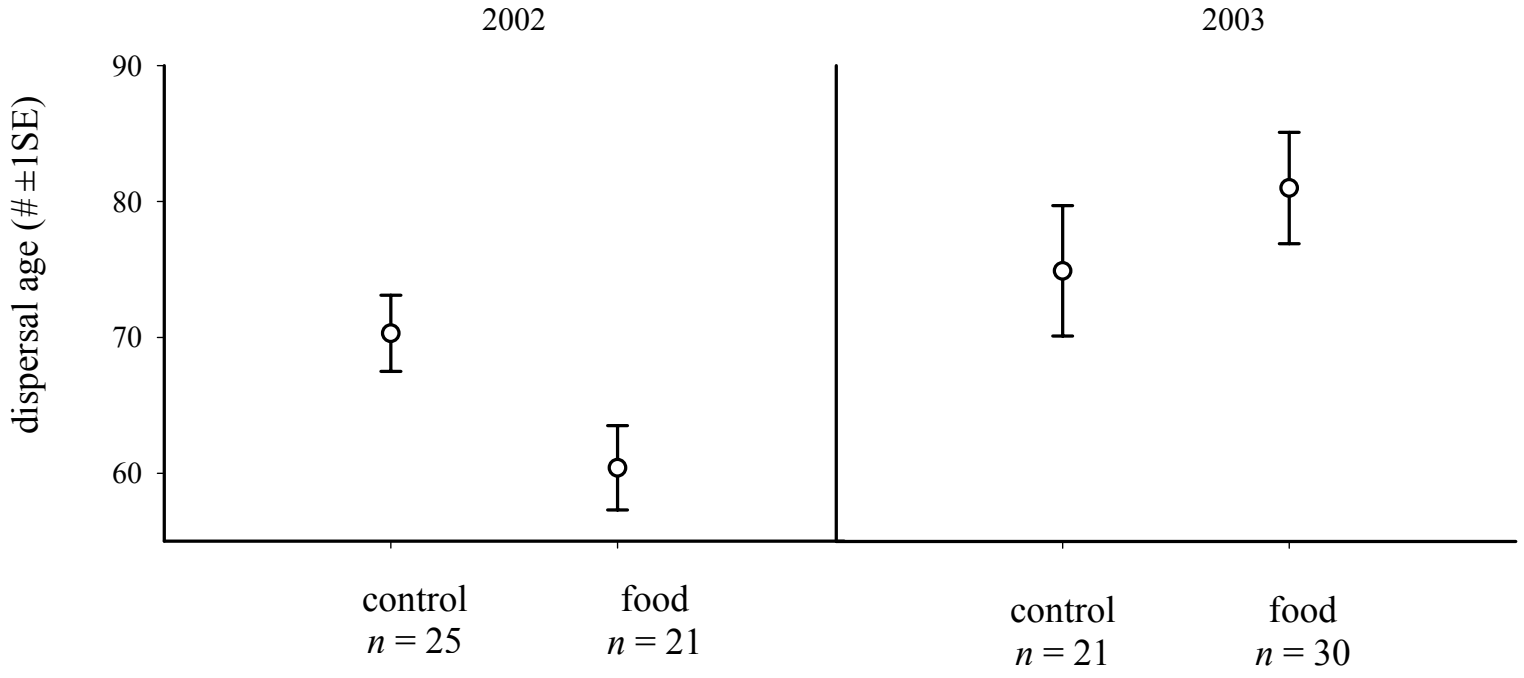


Figure 8: Least squares mean ages (in days; ±1 SE) after controlling for hatch date and parental departure (age of radio-collared juvenile on date the second of its parents departed their natal area) that radio-collared juvenile burrowing owls initiated natal dispersal at nests that were repeatedly treated for ectoparasites with diatomaceous earth (insecticide) and at control nests (control) in eastern Washington in 2002 ($P = 0.348$) and 2003 ($P = 0.024$).

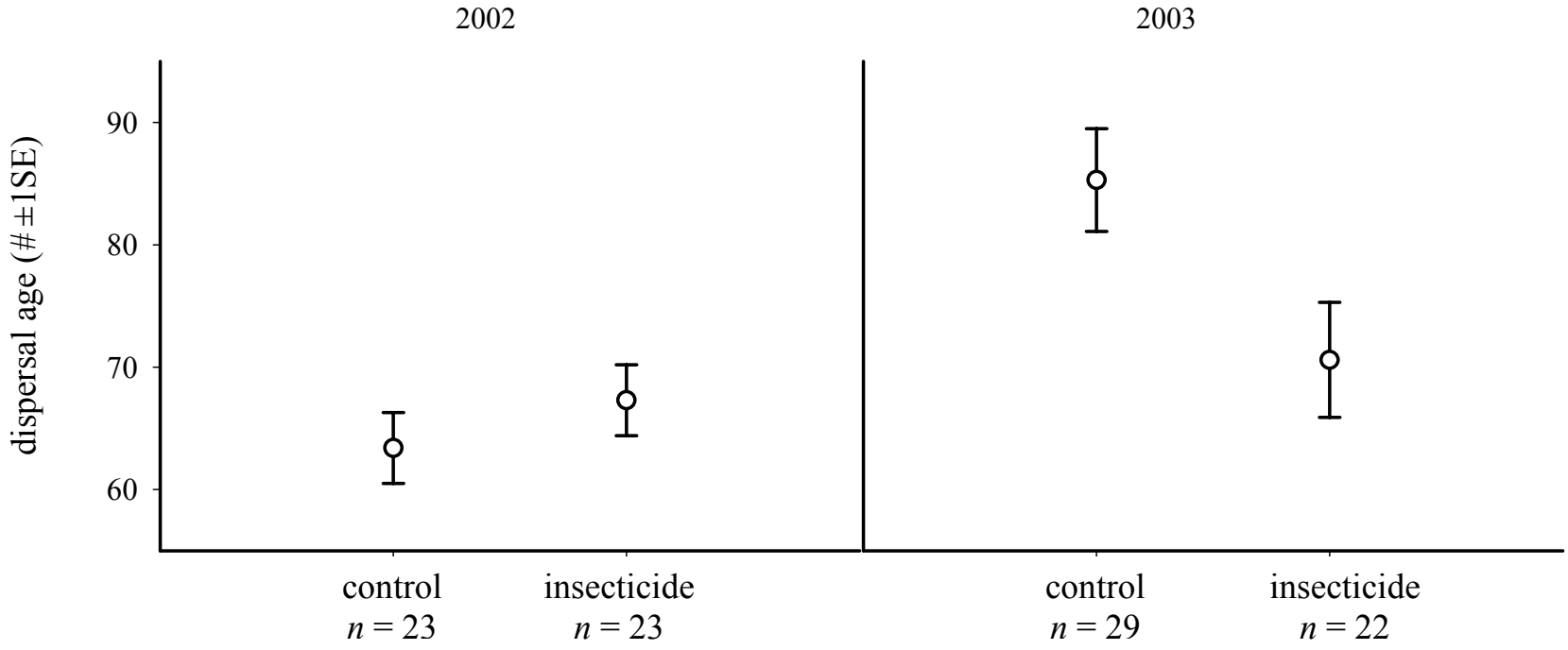


Figure 9. Association between body mass (g) and age (in days) of radio-collared juvenile burrowing owls at nests that were repeatedly supplemented with laboratory mice (food) and at control nests (control) in eastern Washington in 2002 ($P = 0.118$) and 2003 ($P = 0.014$).

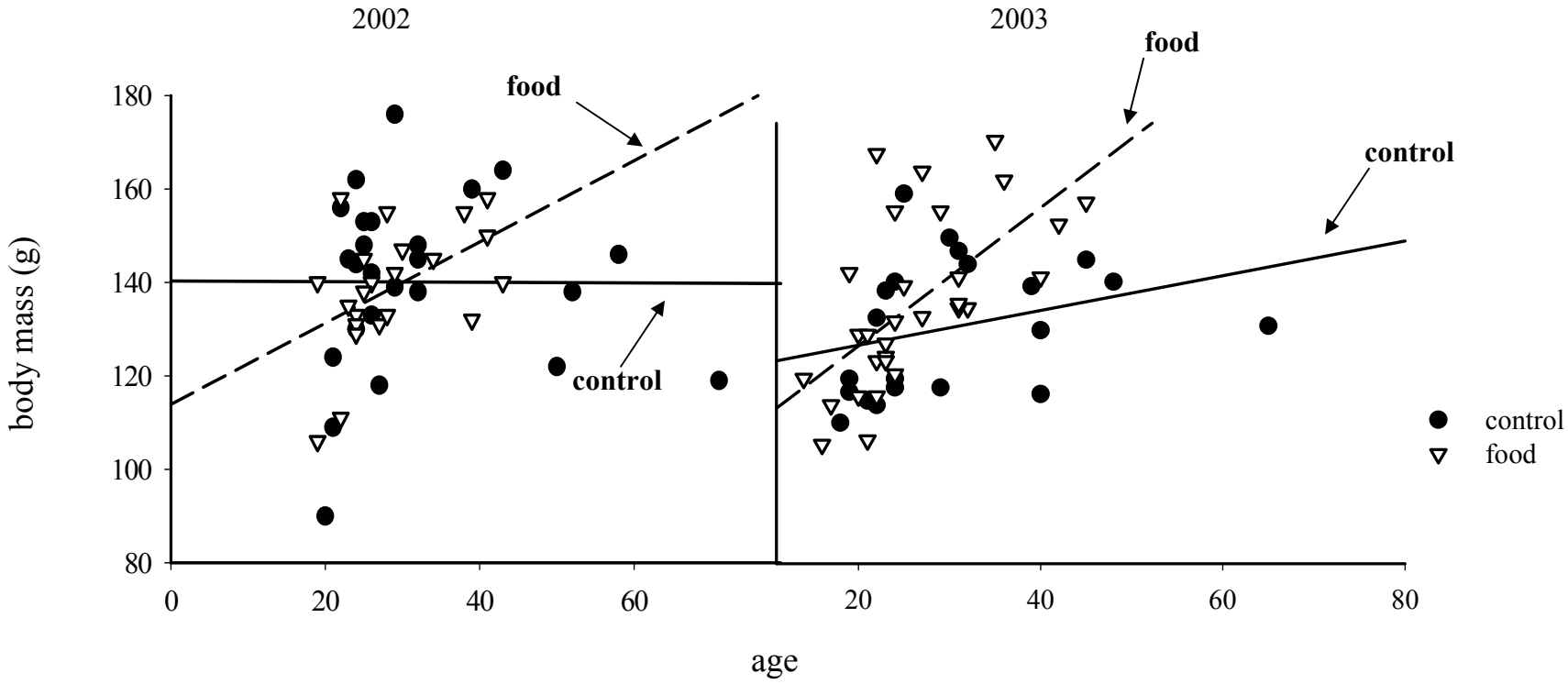


Figure 10. Index of flea load (0-5; 0 = 0 fleas, 5 = >15 fleas; ±1 SE) assigned to radio-collared juvenile burrowing owls based on number of ectoparasites (usually fleas) visible on juveniles at nests that were repeatedly treated with diatomaceous earth (insecticide) and at control nests (control) in eastern Washington in 2002 ($P = 0.509$) and 2003 ($P = 0.064$).

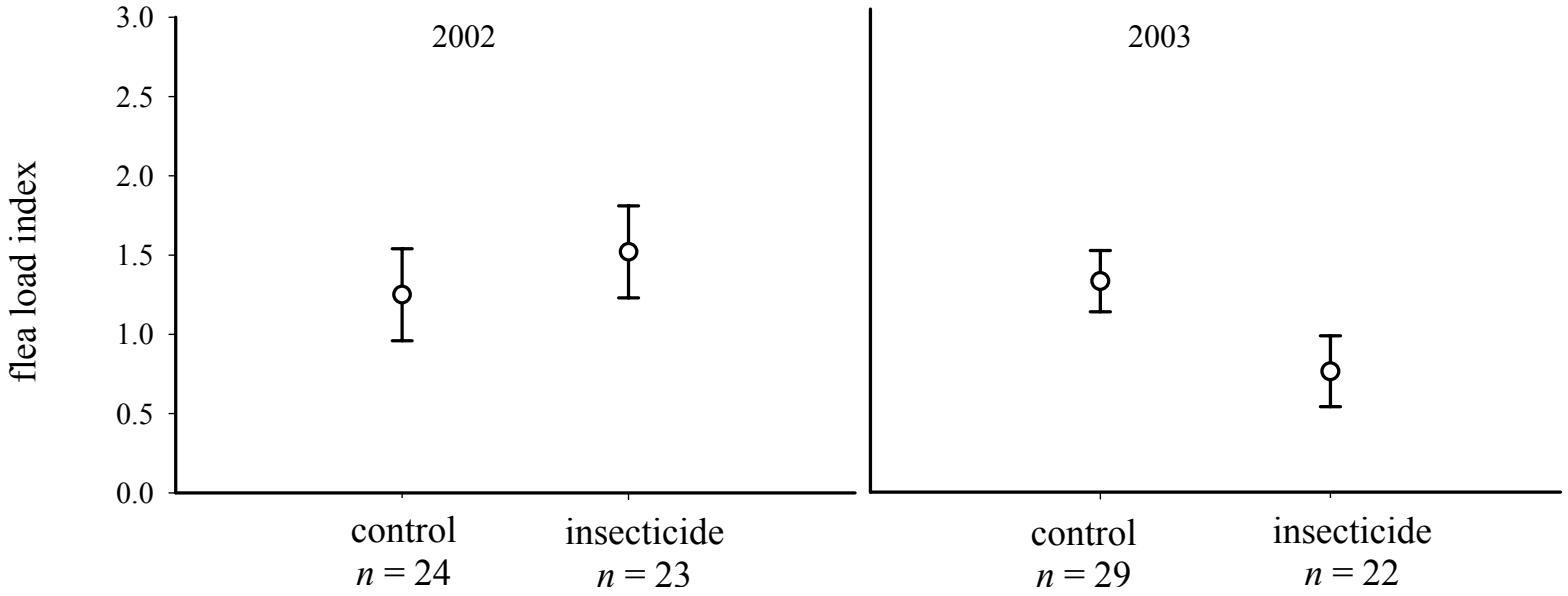


Figure 11. Relative small mammal abundance (1+ number of small mammals captured at burrowing owl nests; ±1 SE) per trapping session in eastern Washington in 2002 ($P < 0.0001$) and 2003 ($P = 0.127$). Each trapping session consisted of 2 trapping nights.

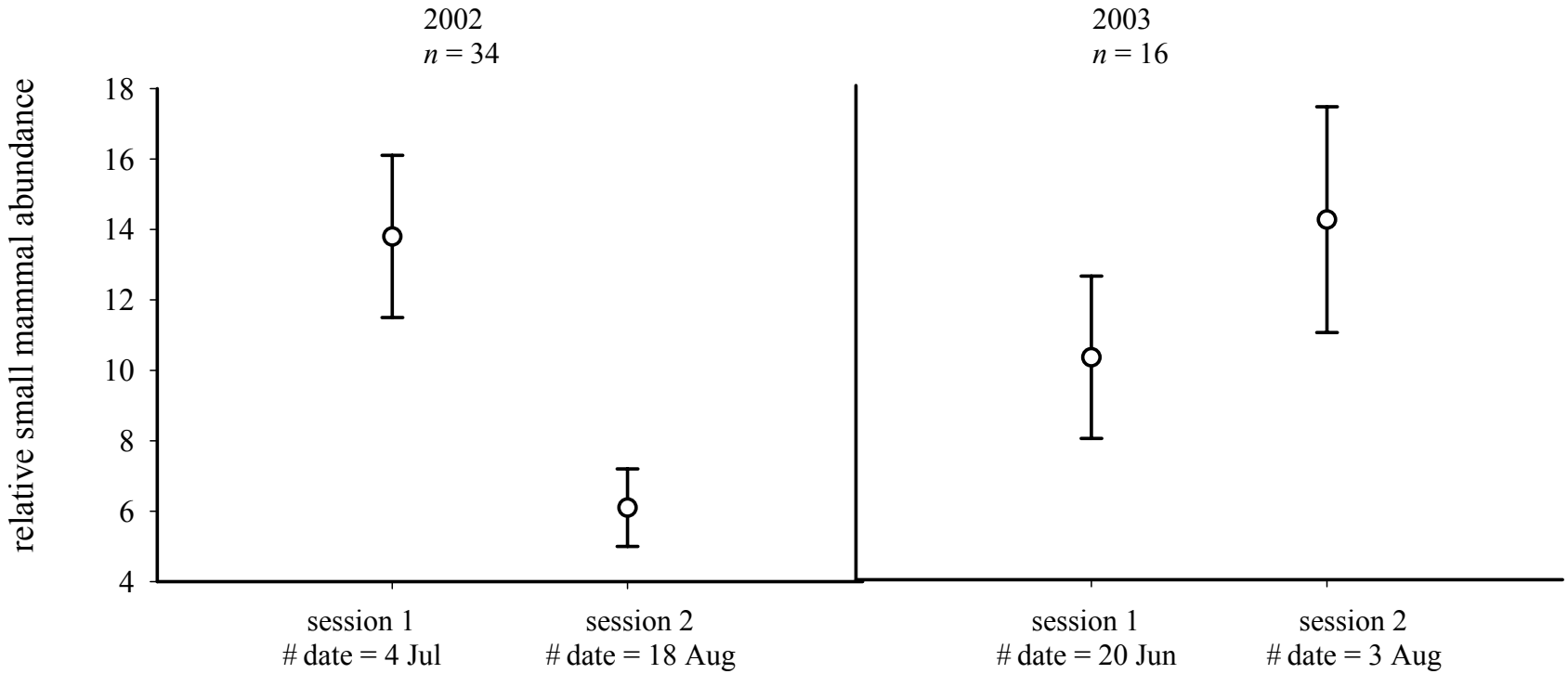


Figure 12. Association between dispersal age (in days) of juvenile burrowing owls and relative small mammal abundance (1+ number of small mammals captured at burrowing owl nests) in eastern Washington in 2002 ($P = 0.774$) and 2003 ($P = 0.079$).

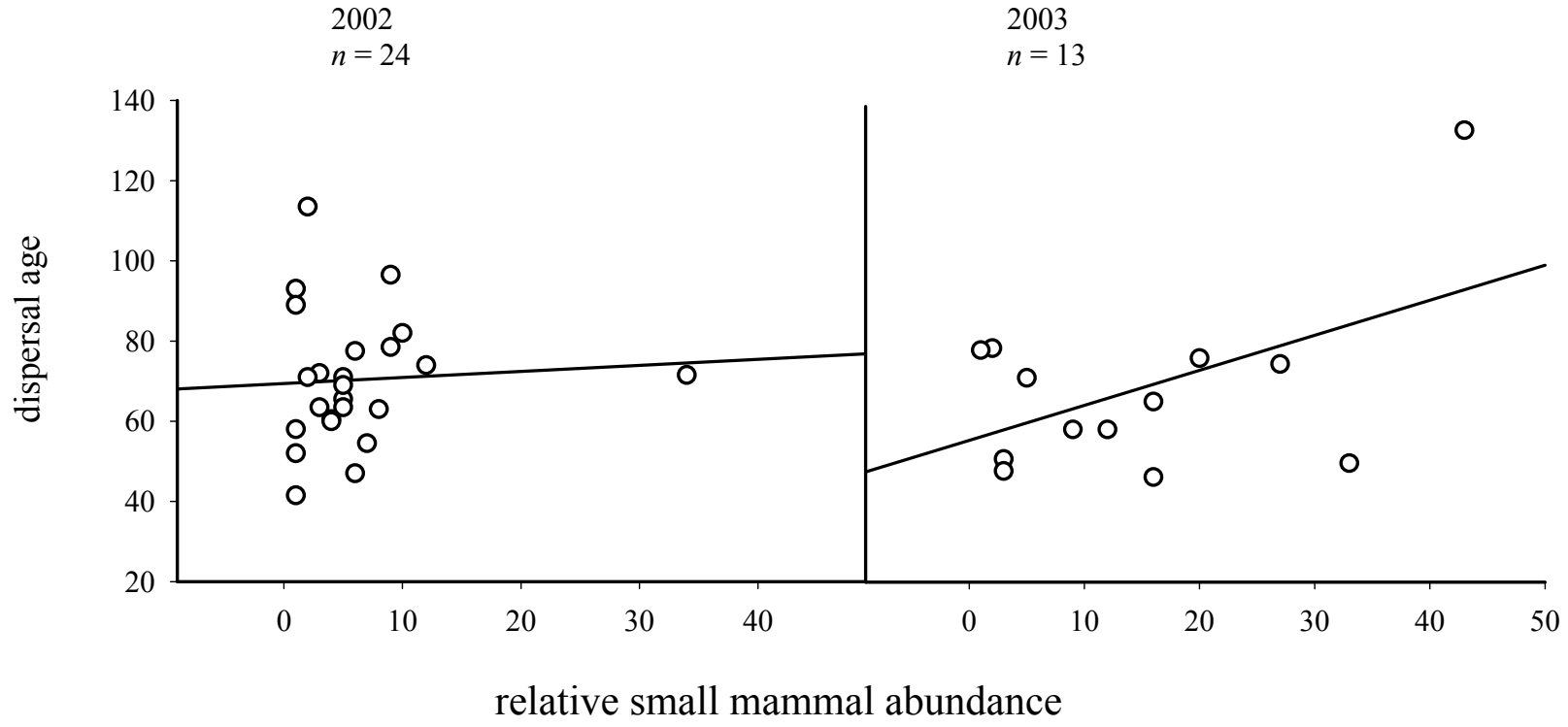


Figure 13. Association between parental departure (age of radio-collared juvenile on date the second of its parents departed their natal area) of burrowing owls and relative small mammal abundance (1+ number of small mammals captured at burrowing owl nests) in eastern Washington in 2002 ($P = 0.217$) and 2003 ($P = 0.0008$).

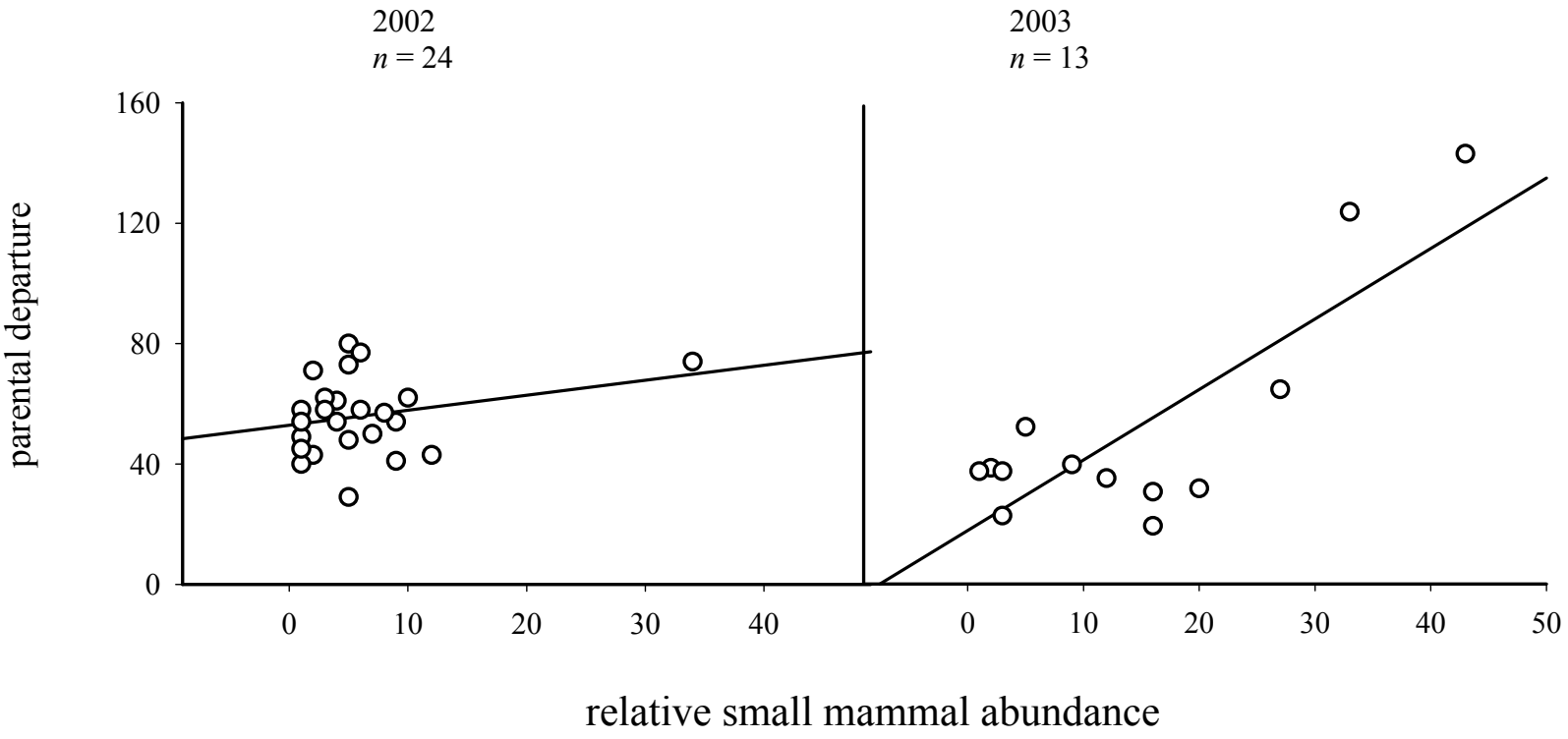


Figure 14. Index of flea load (0-5; 0 = 0 fleas, 5 = >15 fleas; ±1 SE) assigned to radio-collared juvenile burrowing owls based on number of ectoparasites (usually fleas) visible on the juvenile in eastern Washington in 2002 and 2003 ($P = 0.211$).

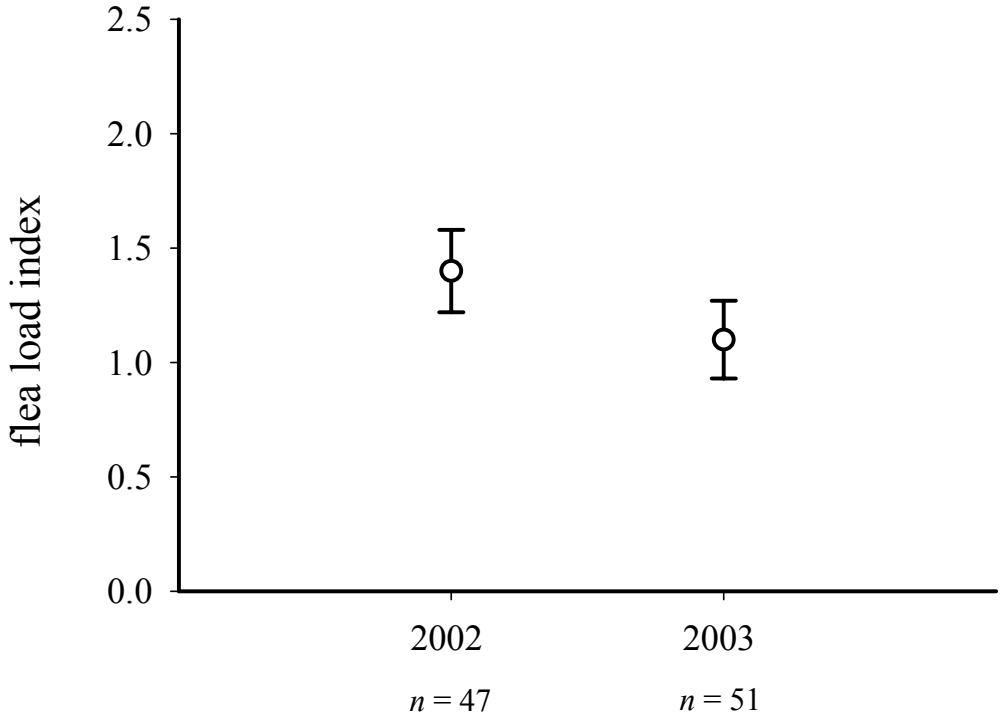
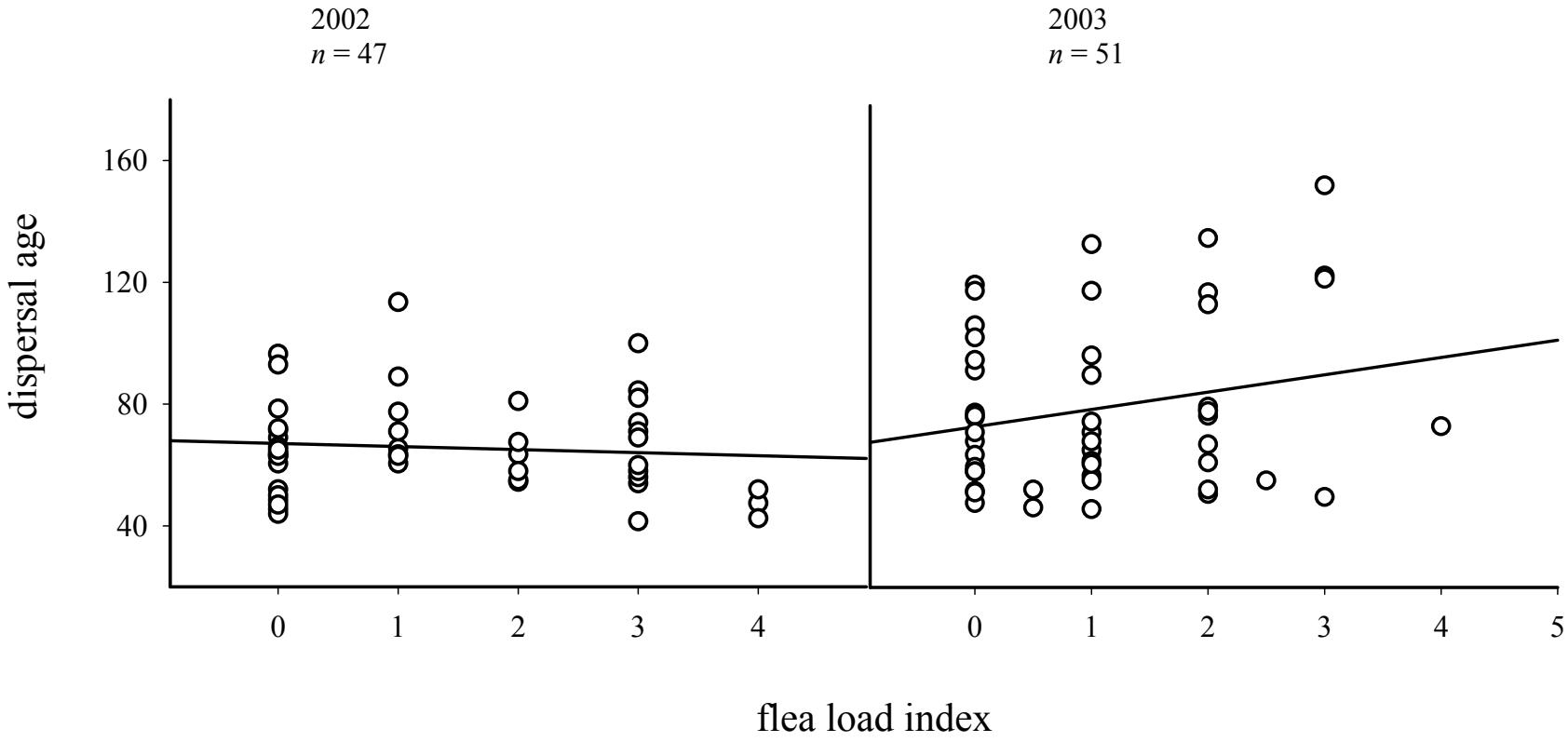


Figure 15. Association between index of flea load (0-5; 0 = 0 fleas, 5 = >15 fleas) assigned to radio-collared juvenile burrowing owls based on number of ectoparasites (usually fleas) visible on the juvenile and dispersal age (in days) of radio-collared juvenile burrowing owls in eastern Washington in 2002 ($P = 0.553$) and 2003 ($P = 0.115$).



APPENDIX A. Protocol for sexing burrowing owls using blood DNA.

Methods:

I obtained burrowing owl blood stored in EDTA buffer, which was then transferred to lysis buffer at the Genomic Analysis and Technology Core (GATC) at the University of Arizona. I isolated total DNA by overnight lysis with proteinase K at 55°C, followed by extraction using phenol/chloroform and isopropanol/sodium acetate precipitation following the protocol of Goldberg et al ("From the frog's mouth: buccal swabs for collection of DNA from amphibians," *Herpetological Review*, 35. 2003). I resuspended the DNA in low TE (10 mM Tris pH 8.0, 0.01 mM EDTA) and quantified it using a FLx 800 Microplate Fluorescence Reader (Bio-Tek Instruments, Inc.). I diluted working stock solutions to 5 ng/µl.

I used a polymerase chain reaction (PCR) to amplify regions on the avian sex chromosome using a Mastercycler® gradient (Eppendorf Scientific, Inc.). I performed an amplification in 10 µl reaction volume containing 0.2 µM of each primer, 10 mM Tris-HCl (pH 8.3), 0.25 mM of each dNTP, 0.4 units of *Taq* (Sigma-Aldrich), 50 mM KCl, 5 ng of genomic DNA, and 2.5 µM $MgCl_2$. The cycling was; initial denature 94º for 3 minutes, denature 94º for 30 seconds, anneal 54º for 1 minute, extension 72º for 2 minutes, and final extension of 72º for 3 minutes and allowed the PCR to run for 35 cycles. The primers I used where 5' GTT ACT GAT TCG TCT ACG AGA and 5' ATT GAA ATG ATC CAG TGC TTG which were published by Fridolfsson and Ellengren ("A simple and universal method for molecular sexing of non-ratite birds" Journal of Avian Biology 30:116-121, 1999).

I visualized PCR product using 2% agarose gel and stained with GelStar® Nucleic Acid Gel Stain (Cambrex Bio Science Rockland, Inc.). The sex of the birds was determined based on females having two bands at about 600 bp and 1150 bp, and males having only one band at 600 bp.

Title: Juvie Owl backlog from batch 1 + batch 2
Researcher: Christine

Date: 7/22/04
Primers: Mai 1, Mai 2

	Initial Denature	Denature	Anneal	Extention	Final Extention
Temp	94	94	54	72	72
Time	3 min	30 sec	1 min	2 min	3 min

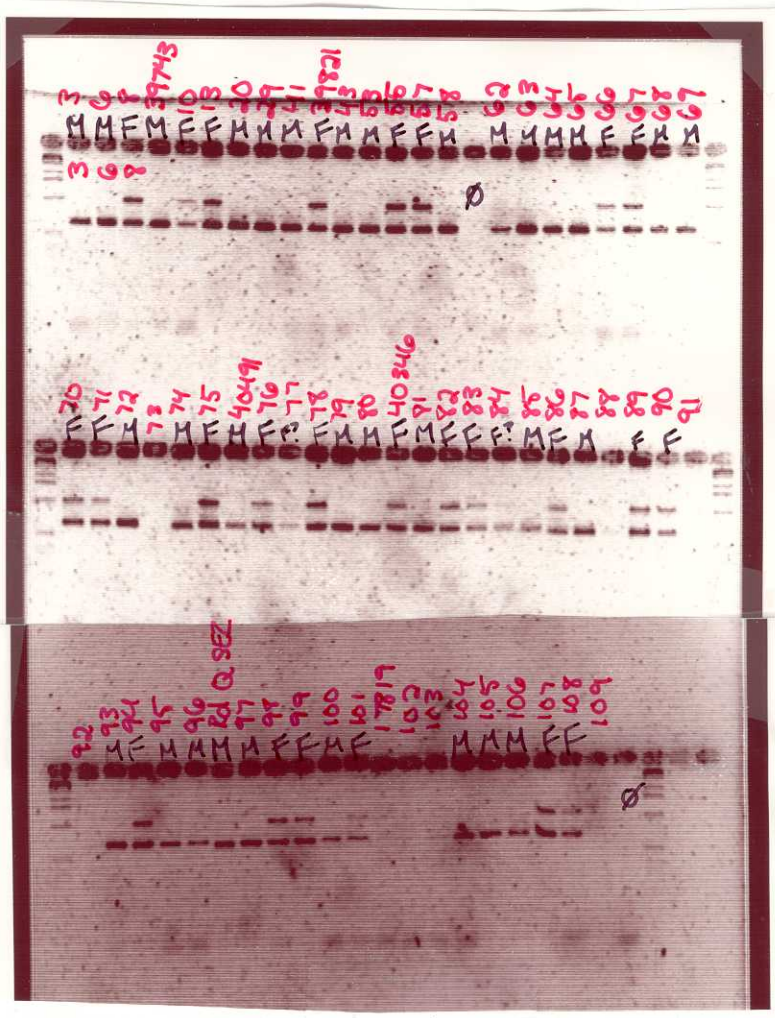
Cycler	Gradient
# Cycles	35

Master Mix		# Rxns 72	
H20	7.27		523.44
Buffer D 10x	1		72
dNTPs (2.0mM)	1.25		90.00
Primer 1 (Mai 1)	0.2		14.40
Primer 2 (Mai 2)	0.2		14.40
Taq polymerase	0.08		5.76
Total master mix			**720**
DNA	1		

Add 9 µl master mix

39743 male
Rd Q SEZ male
39821 female
40491 male
40346 female
17819 female

Owl 003	Owl 041	Owl 062	Owl 070	Owl 077	Owl 084	Owl 092	Owl 099	Owl 106			
Owl 006	**39821**	Owl 063	Owl 071	Owl 078	Owl 085	Owl 093	Owl 100	Owl 107			
Owl 008	Owl 043	Owl 064	Owl 072	Owl 079	Owl 086	Owl 094	Owl 101	Owl 108			
39743	Owl 053	Owl 065	Owl 073	Owl 080	Owl 087	Owl 095	**17819**	Owl 109			
Owl 010	Owl 055	Owl 066	Owl 074	**40346**	Owl 088	Owl 096	Owl 102	H20			
Owl 013	Owl 057	Owl 067	Owl 075	Owl 081	Owl 089	**Rd Q SEZ**	Owl 103				
Owl 020	Owl 058	Owl 068	**40491**	Owl 082	Owl 090	Owl 097	Owl 104				
Owl 029	H20	Owl 069	Owl 076	Owl 083	Owl 091	Owl 098	Owl 105				



Title: Juvie Owl #001-061
Researcher: Christine

Date: 7/13/04
Primers: Mai 1, Mai 2

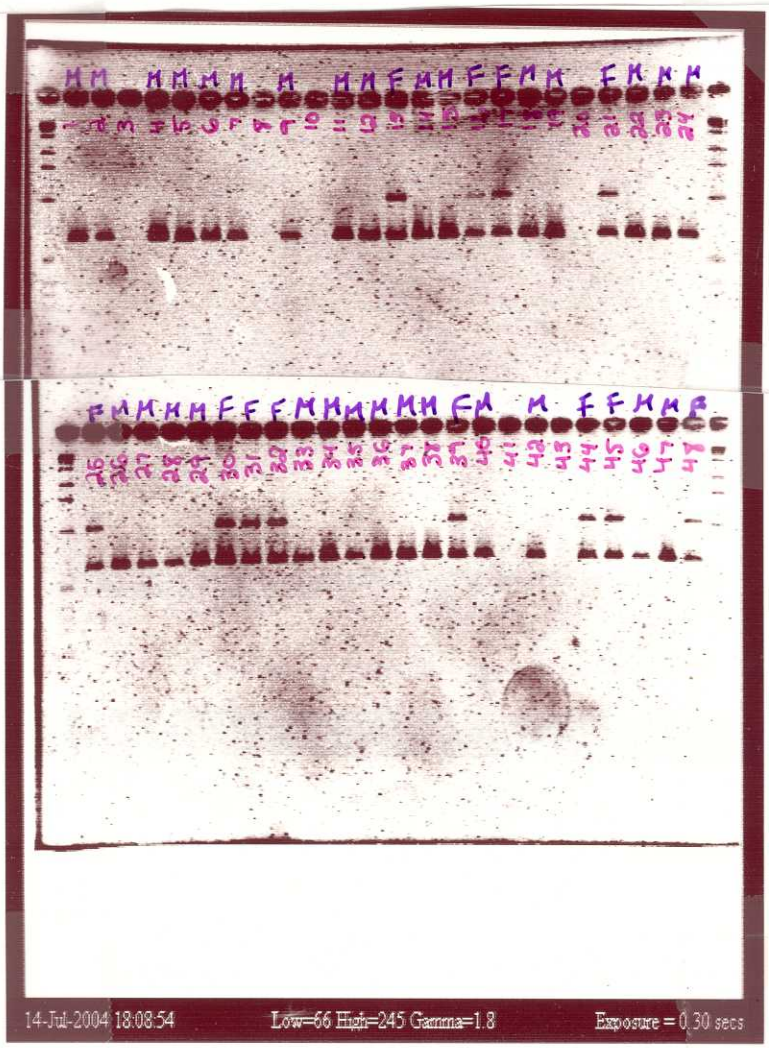
	Initial Denature	Denature	Anneal	Extention	Final Extention
Temp	94	94	54	72	72
Time	3 min	30 sec	1 min	2 min	3 min

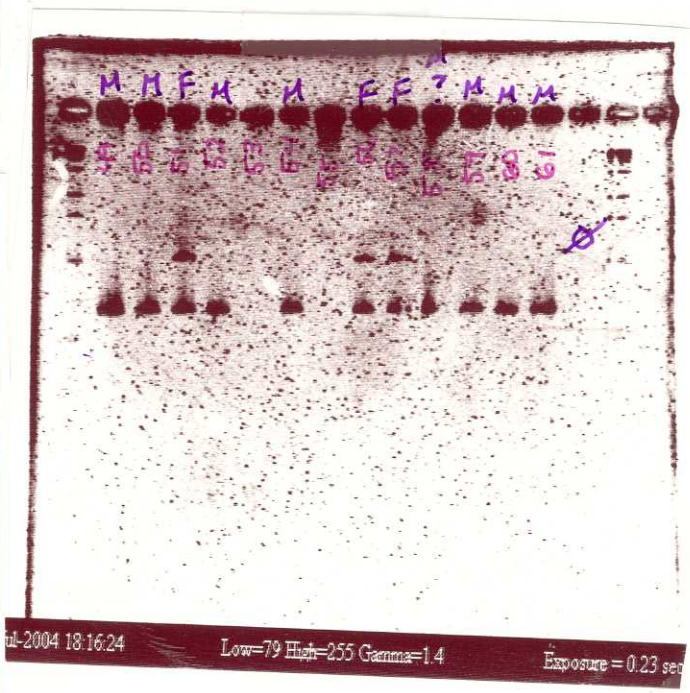
Cycler	Gradient
# Cycles	35

Master Mix		# Rxns 67.1	
H20	7.27		487.82
Buffer D 10x	1		67.1
dNTPs (2.0mM)	1.25		83.88
Primer 1 (Mai 1)	0.2		13.42
Primer 2 (Mai 2)	0.2		13.42
Taq polymerase	0.08		5.37
Total master mix			**671**
DNA	1		

Add 9 µl master mix

Owl 001	Owl 009	Owl 017	Owl 25	Owl 33	Owl 41	Owl 49	Owl 57				
Owl 002	Owl 010	Owl 018	Owl 26	Owl 34	Owl 42	Owl 50	Owl 58				
Owl 003	Owl 011	Owl 019	Owl 27	Owl 35	Owl 43	Owl 51	Owl 59				
Owl 004	Owl 012	Owl 020	Owl 28	Owl 36	Owl 44	Owl 52	Owl 60				
Owl 005	Owl 013	Owl 021	Owl 29	Owl 37	Owl 45	Owl 53	Owl 61				
Owl 006	Owl 014	Owl 022	Owl 30	Owl 38	Owl 46	Owl 54	H20				
Owl 007	Owl 015	Owl 023	Owl 31	Owl 39	Owl 47	Owl 55					
Owl 008	Owl 016	Owl 024	Owl 32	Owl 40	Owl 48	Owl 56					





Title: Juvie Owl backlog from batch 2
Researcher: Christine

Date: 7/27/04
Primers: Mai 1, Mai 2

	Initial Denature	Denature	Anneal	Extention	Final Extention
Temp	94	94	54	72	72
Time	3 min	30 sec	1 min	2 min	3 min

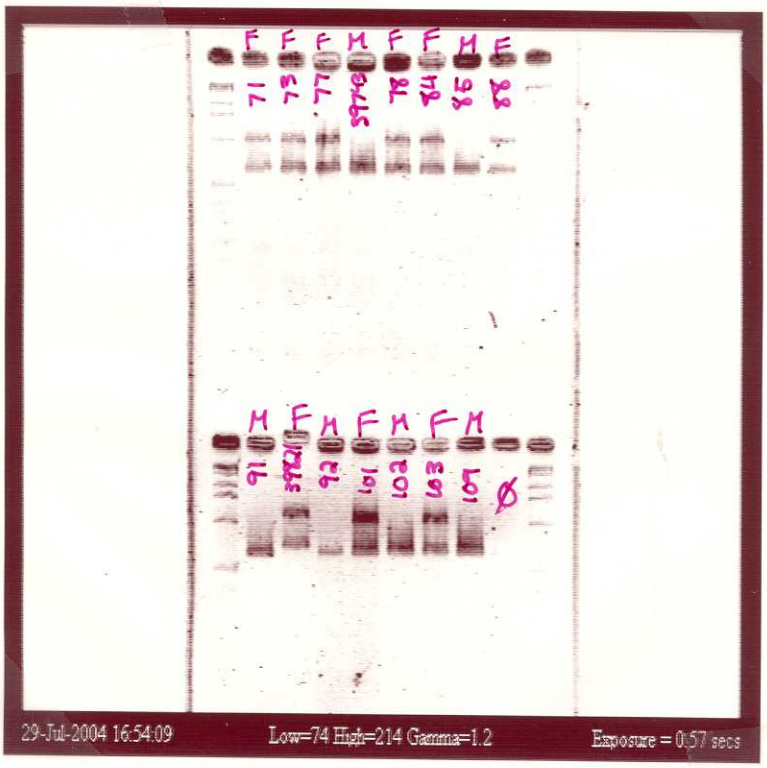
Cycler	Gradient
# Cycles	35

Master Mix		# Rxns 18	
H20	7.27		130.86
Buffer D 10x	1		18
dNTPs (2.0mM)	1.25		22.50
Primer 1 (Mai 1)	0.2		3.60
Primer 2 (Mai 2)	0.2		3.60
Taq polymerase	0.08		1.44
Total master mix			**180**
DNA	1		

Add 9 µl master mix

39743 male
Rd Q SEZ male
39821 female
40491 male
40346 female
17819 female

Owl 071	Owl 091										
Owl 073	**39821**										
Owl 077	Owl 092										
39743	Owl 101										
Owl 078	Owl 102										
Owl 084	Owl 103										
Owl 085	Owl 109										
Owl 088	H20										



APPENDIX B. Institutional Animal Care and Use Committee

This study was approved by the University of Arizona Institutional Animal Care and Use Committee protocols #01-089 and #03-052.

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