

Marine subsidies alter the diet and abundance of insular and coastal lizard populations

Kyle Barrett, Wendy B. Anderson, D. Alexander Wait, L. Lee Grismer, Gary A. Polis[†] and Michael D. Rose[†]

Barrett, K., Anderson, W. B., Wait, D. A., Grismer, L. L., Polis, G. A. and Rose, M. D. 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations. – *Oikos* 109: 145–153.

We evaluated the impact of marine materials on the diet and abundance of arthropodivorous lizards inhabiting islands and the coast of the Gulf of California. Here, marine materials are brought onto land by seabirds and by tidal action, and both subsidy pathways cause arthropod abundance to increase. We evaluated *Uta stansburiana* (side-blotched lizard) diets in three habitats defined by having: (1) no marine subsidies available, (2) only seabird-derived subsidies, and (3) only tidal-derived subsidies. Stable isotope data indicated that lizard diets are subsidized indirectly by seabird and tidal activity. For example, in coastal areas we determined that 40% of a lizard's diet contains arthropods that have consumed algae. Such subsidies may explain why we found that lizards in coastal areas occupy a significantly higher trophic position than lizards in unsubsidized areas. We analyzed eight years of survey data on all arthropodivorous lizards to determine if diet subsidies result in increased lizard abundance. We found that lizards were more abundant in coastal areas than they were in inland habitats, and that they were more abundant on islands with seabirds than on islands without seabird populations. This study provides insight into the importance and effect of marine-derived nutrients from multiple sources on vertebrate consumers inhabiting islands and coastal areas.

K. Barrett and D. A. Wait, Dept of Biology, Southwest Missouri State Univ., Springfield, MO 65804, USA. Present address for KB: Dept of Biological Sciences, 331 Funchess Hall, Auburn Univ., Auburn, AL 36849-5414, USA (barrerck@auburn.edu). – W. B. Anderson, Biology Dept, Drury Univ., Springfield, MO 65807, USA. – L. L. Grismer, Dept of Biology, La Sierra Univ., Riverside, CA 92515, USA. – G. A. Polis and M. D. Rose, deceased, 27 March 2000.

Ecosystems, even those with seemingly distinct borders, rarely function independent of other adjacent ecosystems. Ecologists are increasingly recognizing the important effects that cross-ecosystem transport of energy and nutrients have on plant and animal population and community patterns (Wiens 1992, Polis and Hurd 1996a, Polis et al. 1997, Huxel and McCann 1998, Hilderbrand et al. 1999). The transport of energy and nutrients occurs from organisms that travel across ecosystem boundaries (Hilderbrand et al. 1999, Nakano et al. 1999, Bouchard and Bjorndal 2000) or from abiotic factors such as wind,

tidal action, or watershed drainage (Gasith and Hasler 1976, Jansson et al. 2000).

When materials move from a highly productive system to a relatively unproductive system, they have the greatest potential to alter plant and animal population and community dynamics (Polis and Hurd 1995, Anderson and Polis 1999). For example, while the Gulf of California is extremely productive ($536 \text{ g m}^{-2} \text{ yr}^{-1}$ dry mass; Maulf 1983), nearby terrestrial productivity is quite low ($0\text{--}60 \text{ g m}^{-2} \text{ yr}^{-1}$ dry mass; Anderson and Wait 2004, Wait et al. 2004). Materials are transferred from the

Accepted 11 October 2004

Copyright © OIKOS 2005
ISSN 0030-1299

ocean onto the islands and mainland coast by two mechanisms (Polis and Hurd 1996a). Tidal activity washes large algal mats and marine carrion onto the beaches of the islands and mainland. Seabirds, which feed exclusively in the marine system, transport marine-derived nutrients onto the islands when they return to roost and nest (Hutchinson 1950, Sobey and Kenworthy 1979, Polis and Hurd 1996a). These nutrients may be in the form of guano, fish scraps, eggs, or bird carcasses. These marine materials have been found to subsidize insular and coastal communities including plants (Anderson and Polis 1999), detritivorous beetles (Sanchez-Piñero and Polis 2000), rodents (Stapp et al. 1999, Stapp and Polis 2003), and spiders and scorpions (Polis and Hurd 1995). For the insular consumers listed above, a positive correlation between population density and marine subsidies has been demonstrated (Polis and Hurd 1995, Stapp et al. 1999, Sanchez-Piñero and Polis 2000).

A correlation between the population density of terrestrial organisms and marine subsidies suggests consumption of marine resources by terrestrial consumers (Polis and Hurd 1995, Sanchez-Piñero 2000); however, a direct measure of subsidy consumption can be made using the stable isotopes of carbon (C) and nitrogen (N) (Stapp and Polis 2003). Stable isotopes have become a popular tool for elucidating patterns of ecosystem function (Hesslein et al. 1991, Wainright et al. 1998, Anderson and Polis 1999, Hilderbrand et al. 1999). They may be used to trace the flow of energy through a system (Peterson et al. 1985, Magnusson et al. 2001), identify the number of trophic levels a system supports (Hesslein et al. 1991), or determine the trophic position of a particular group of organisms (Post 2002).

Here, we used multiple stable isotope analysis and population abundance surveys to examine the hypothesis that insular and coastal populations of *Uta stansburiana* Baird and Girard (side-blotched lizards) in the Gulf of California consume materials derived from the extremely productive marine system, and that these food subsidies alter lizard abundance. We used the stable isotopes of C and N from lizard tissues to determine if lizard diets are ultimately based in the marine food web where subsidies are available. To evaluate subsidies from tidal action and subsidies from seabirds separately, we evaluated lizard diets in areas only receiving one subsidy type.

We predicted coastal populations of lizards consuming algivorous or detritivorous insects would be more enriched in $\delta^{13}\text{C}$ than lizards feeding on inland herbivorous insects as a result of the less negative $\delta^{13}\text{C}$ values in algae compared to terrestrial plants. We also predicted that lizards on islands occupied by seabirds would have higher $\delta^{15}\text{N}$ signatures than lizards on islands without seabird populations as a consequence of the high $\delta^{15}\text{N}$ values associated with seabirds and seabird guano. We

used mixing models to quantify the proportions of lizard diets that were derived from coastal materials. Finally, we predicted an increase in lizard abundance in spatially subsidized areas, but we had no a priori reason to predict that a particular subsidy pathway (tidal action or seabirds) would have a greater impact on lizard abundance than the other.

Methods

Study site

Data for stable isotope analyses were collected from nine islands in the Midriff region of the Gulf of California and the adjacent mainland near Bahía de los Angeles, Baja California, Mexico (28°55' N, 113°30' W). The Midriff region of the Baja California peninsula is one of the driest areas in North America, receiving approximately 59 mm of rainfall annually (Reyes-Coca et al. 1990). The islands in this region represent a variety of geological histories (Gastil et al. 1983) and range in size from 0.02 km² to 9.13 km² (Murphy et al. 2002; Table 1). We classified islands in the system as either Bird or Non-bird islands based on the percent guano cover present on the island (<5% guano cover = Non-bird island). We classified 3 islands as Bird islands and 6 as Non-bird islands. Data from the mainland were grouped with the Non-bird island data (Table 1).

Table 1. Size (Murphy et al. 2002) and presence/absence of roosting or nesting seabirds (Felger and Lowe 1976, Sanchez-Piñero and Polis 2000, L. Grismer, pers. obs.) for islands in the Gulf of California used in this study.

Island	Area (km ²)	Data obtained*
Seabirds present		
Alcatraz	1.20	A
Cholluda	0.02	A
Coloraditio	unknown	A
El Muerto	1.33	A
Las Animas	0.08	A
Partida Norte	1.36	A
Piojo	0.57	A, SI
Raza	0.68	A
San Lorenzo	33.03	A
Flecha	0.13	SI
Cerraja	0.04	SI
Seabirds absent		
Bota	0.09	A, SI
Mainland	A, SI	
Mejia	2.26	A
Mitlan	0.16	A, SI
Pata	0.14	A, SI
Salsipuedes	1.16	A
Smith	9.13	A, SI
Tiburón	1223.53	A
Ventana	1.41	A, SI
Cabeza de Caballo	0.77	SI

*A indicates data for lizard abundance analyses were collected from an island. SI indicates data for stable isotope analyses were collected from an island.

To evaluate lizard abundance in subsidized and unsubsidized areas we expanded our study area to 18 islands and included two coastal and two inland areas of the Baja California peninsula (Table 1). These islands range in size from 0.02 km² to 12323.53 km². The northernmost island, El Muerto, is situated at 30°05'00" N, 114°32'00" W and the southernmost island, Las Animas, is located at 25°05'46" N, 110°33'33" W. Nine of these islands have large roosting or nesting seabird colonies and 9 do not. The mainland sites were located near Bahía de los Ángeles (coordinates above), and La Unica, 16 km east-southeast of Bahía de los Ángeles.

Diet sampling and processing

To determine the diet of the lizard *Uta stansburiana*, we measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in tissue samples from terrestrial plants (N=47), marine algae (N=9), arthropods (N=42), and the lizards (N=72) from both Bird and Non-bird islands and from coastal and inland sites (Appendix A). To evaluate independently the effects of bird subsidies and tidal subsidies, we made comparisons among three mutually exclusive habitats: (1) inland areas on islands (n=6 islands) and the mainland without seabird influence, (2) inland areas on islands with seabird influence (n=3 islands), and (3) coastal habitats on islands (n=6 islands) and the mainland without seabird influence. Coastal habitat was defined by the presence of vegetation (primarily *Salicornia subterminalis* Parish and *Frankenia palmeri* Watson) that is indicative of at least some coastal influence (i.e. high salt tolerance). On average, this habitat is approximately 50 m wide, but variation in topography causes variation in the width of the coastal zone among and within islands. We considered coastal and inland habitats within an island as distinct habitats based on the limited home range of *U. stansburiana* (Tinkle 1967, Doughty et al. 1994). None of the Bird islands in our study have coastline suitable for lizard populations; consequently, we did not collect samples for diet analysis from the coast of islands with seabirds.

Stable isotope analysis

Carbon stable isotope values change very little among trophic levels (Peterson et al. 1985, Post 2002). Carbon derived from marine sources (e.g. macroalgae) has a stable isotope ratio more enriched in ¹³C than C derived from terrestrial sources by C₃ plants (*Salicornia subterminalis*, *Frankenia palmeri*), which dominate the coast of the study islands. Consequently, it is possible to use stable isotope ratios to differentiate between C incorporated into insular and coastal organisms that

was ultimately derived from the marine system and C derived in situ from the terrestrial system.

The stable isotopes of N are useful in the Gulf of California insular and coastal systems to identify areas of seabird influence (Anderson and Polis 1998, Wainright et al. 1998). $\delta^{15}\text{N}$ values fractionate as they move through a food web. This is a result of differential protein synthesis and excretion of the isotopically light ¹⁴N (Ponsard and Averbuch 1999). Consequently, $\delta^{15}\text{N}$ values increase approximately 3.4‰ with each trophic transfer (Post 2002). Seabirds occupy a relatively high trophic level and therefore have elevated $\delta^{15}\text{N}$ values. Organisms utilizing N directly from seabird tissue will develop an even higher $\delta^{15}\text{N}$ value (Wainright et al. 1998). Seabird guano often has a $\delta^{15}\text{N}$ value greater than seabird tissue. This high value results from a rapid mineralization of the uric acid in guano to ammonium (NH₄). Subsequently, the NH₄ is subject to volatilization (Lindeboom 1984), which results in a large isotopic fractionation (Wainright et al. 1998). As a result, plants that are fertilized from bird guano have $\delta^{15}\text{N}$ values that are distinctly high (Anderson and Polis 1999). Species with diets immediately or ultimately based on plants fertilized by guano, dead seabirds, or seabird guano would be expected to have distinguishably higher $\delta^{15}\text{N}$ signatures than herbivorous and detritivorous species in areas without seabird activity.

We used models designed for stable isotope data to quantify further the effects of marine subsidies on the diet of *U. stansburiana*. We used two-end-member mixing models (Gannes et al. 1997, Wolf et al. 2002) in coastal areas on Non-bird islands to determine percent use by *U. stansburiana* of C derived from algae and C₃ plants. Algae and C₃ plants are the only basal resources in the coastal area; consequently, the two-end member mixing model was the appropriate choice to characterize the importance of possible C sources to coastal lizards. We could not use a two-end-member mixing model on seabird islands because of the availability of more than two C sources (i.e. seabird tissue, guano, C₃ plants, and C₄ plants; Peterson et al. 1985). We also used a trophic position model (Post 2002) to compare the trophic position of coastal lizards to that of inland lizards. Trophic position provides a measure of the location of a species within the food web and its value may be a non-integer (Post 2002). Appendix A provides a description of the models used for this study.

Lizard abundance surveys

To evaluate a potential population level effect of marine inputs into coastal and insular areas, we measured the abundance of arthropodivorous lizards. All arthropodivorous lizards were considered for this analysis, thus we are assuming that lizards other than *U. stansburiana*

consume subsidized arthropods when they are available. Lizards were surveyed on Bird islands in coastal and inland areas and on Non-bird islands in coastal and inland areas on 18 islands in the Gulf and at 4 sites on the mainland. The access to islands not available during the stable isotope study allowed us to include a fourth habitat type (i.e. the coast of Bird islands). Surveys took place from 1992–1997 and during 2001 and 2002. Observers performed all surveys in late May and early June between 9:30 am and 2:30 am (when lizards were most active). To estimate lizard abundance, trained observers walked in nonoverlapping areas within a designated habitat type and recorded the number of lizards sighted. These values were standardized as number of lizards sighted/person search hour (Case 1983 for a review). We scaled observation times to habitat and/or island area (i.e. larger islands and habitats were surveyed longer). On Bird islands coastal habitats were surveyed for a total of 9.3 hours, and inland habitats were surveyed for 12.2 total hours. On Non-bird islands and the mainland, coastal habitats were surveyed for 10.6 total hours, and inland habitats were surveyed for 40.3 total hours. In sum, we performed lizard surveys for 72.4 hours.

Data analysis

To determine if we could combine stable isotope data from different sampling periods (Appendix A), we compared lizard stable isotope values using a one-way analysis of variance (ANOVA). We found no significant difference ($p > 0.05$) among the three dates for lizard samples. We did not collect arthropod and plant samples from all habitats on all dates; therefore, we used two-sample t-tests as needed to determine if data collected from a habitat over more than one date could be combined. All comparisons yielded nonsignificant results ($p > 0.05$), so combined data are used for all analyses.

We used a one-way ANOVA to compare tissue samples taken from the three habitat types for plants, arthropods, and lizards. We plotted plant and arthropod isotope values with lizard samples from the same island type (Bird or Non-bird island) and habitat (coast or inland) to determine if these lower trophic levels link lizards to the marine food web. We used an ANOVA with a split-plot design to compare abundance data for lizards among the habitat types outlined above. Abundance data were log-transformed to meet the assumption of normality. For the analysis each island was treated as a random factor, and survey location (coast or inland) as a fixed-effect, subplot factor. Island was nested under the main plot factor, island type (Bird or Non-bird). The year in which each survey was taken could not be considered in the analysis, as each island was not

surveyed every year. We also used simple linear regression to analyze the relationship between island size and lizard abundance.

All data analyses were performed in Minitab 13.1 (Minitab Inc., State College, PA). Means are reported \pm standard error. We considered p -values < 0.05 to be significant.

Results

Stable isotope analysis of *U. stansburiana* diets

The $\delta^{13}\text{C}$ signatures for the primary producers in the system varied predictably by photosynthetic pathway (Table 2). C_3 and C_4 plants on bird islands had significantly greater $\delta^{15}\text{N}$ values than plants with the same photosynthetic pathway in both coastal and inland habitats (Table 2).

Arthropods did not differ significantly among habitat types with respect to $\delta^{13}\text{C}$ values (Table 2, Fig. 1). Arthropods on islands with seabird populations had significantly greater $\delta^{15}\text{N}$ values than populations in coastal and inland habitats (Table 2, Fig. 1). Because we combined detritivorous, herbivorous, and carnivorous arthropods for stable isotope analysis, and each of these feeding guilds has a unique range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, within habitat variance was often quite high (Table 2).

Lizard populations in seabird-influenced areas, in coastal areas, and in inland areas without access to subsidies had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that were significantly different from one another (Table 2, Fig. 1). Mean lizard isotopic values for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were very similar to the mean values for arthropods in each of the three habitat types (Fig. 1).

In coastal habitats, the two-end-member mixing model indicated that, on average, 40% (range = 9–100%) of a lizard's diet contains arthropods that have consumed algae. The trophic position model used in coastal and inland habitats on islands without seabirds indicated lizards in coastal habitats occupied a trophic position of 3.3 ± 0.4 , while inland populations held a slightly lower position of 2.7 ± 0.2 . The trophic position estimate for coastal populations was significantly greater than that for inland populations (one-tailed t-test; $df = 42$, $t = 1.81$, $p = 0.04$).

Lizard abundance surveys

Overall lizard abundance varied from 0.4 lizards sighted hr^{-1} (Isla Mitlan, a Non-bird island) to 214.5 lizards sighted hr^{-1} (Isla Raza, a Bird island). Lizard abundance was significantly greater on the coast than in inland habitats, and on Bird islands relative to Non-bird islands (Fig. 2, Table 3). Median lizard abundance on the

Table 2. Means \pm standard errors and ANOVA values for the stable isotope results from organisms in subsidized and unsubsidized habitats on desert islands and the mainland in the Midriff region of the Gulf of California. Sample sizes are provided in parentheses. Alphabetical superscripts across rows represent the results from Tukey's pairwise comparison. BRD = inland areas on islands with seabird populations; CST = coastal areas on islands and the mainland without seabird populations; INL = inland areas on islands and the mainland without seabird populations.

Organism	BRD	CST	INL	df	MS	F	p-value
$\delta^{13}\text{C}_{\text{‰}}$							
Algae		-12.1 \pm 1.2 (9)					
C ₃ plants	-23.8 \pm 0.4 (12)	-23.9 \pm 0.6 (4)	-24.4 \pm 0.3 (6)	2, 19	0.84	0.64	0.54
C ₄ plants	-13.9 \pm 0.2 (11)	-13.9 \pm 0.1 (5)	-14.0 \pm 0.2 (7)	2, 20	0.007	0.02	0.98
Arthropods	-15.3 \pm 1.1 (7)	-18.3 \pm 1.0 (25)	-18.7 \pm 1.0 (9)	2, 38	28.2	1.44	0.25
<i>U. stansburiana</i>	-13.0 \pm 0.3 (28) ^a	-18.9 \pm 0.8 (14) ^b	-16.9 \pm 0.2 (30) ^c	2, 63	181.1	67.31	<0.0005
$\delta^{15}\text{N}_{\text{‰}}$							
Algae		12.4 \pm 0.5 (9)					
C ₃ plants	24.5 \pm 1.1 (12) ^a	8.2 \pm 2.1 (4) ^b	6.8 \pm 1.1 (6) ^b	2, 19	800.5	62.8	<0.0005
C ₄ plants	24.3 \pm 1.4 (11) ^a	14.5 \pm 3.5 (5) ^b	7.8 \pm 1.2 (7) ^b	2, 20	607.4	23.1	<0.0005
Arthropods	27.8 \pm 3.6 (7) ^a	17.3 \pm 0.7 (25) ^b	13.6 \pm 1.1 (9) ^b	2, 38	425.2	17.9	<0.0005
<i>U. stansburiana</i>	28.8 \pm 0.6 (28) ^a	17.9 \pm 1.1 (14) ^b	13.0 \pm 0.6 (30) ^c	2, 63	1549.1	130.9	<0.0005

coast of Bird islands (62.95 lizards sighted hr⁻¹) was over four times greater than median lizard abundance in the inland areas of Bird islands, and over nine times greater than the median abundance in inland areas of Non-bird islands (Fig. 2). Lizard abundance on the coast of Non-bird islands was also significantly greater than inland abundance on the same island type (Table 3). Island size was a statistically non-significant predictor of lizard abundance for both the Bird and Non-bird island data sets (df = 1, r² = 0.09, p = 0.46; df = 1, r² = 0.02, p = 0.91, respectively).

Discussion

This study demonstrated that insular and coastal populations of an arthropodivorous generalist lizard,

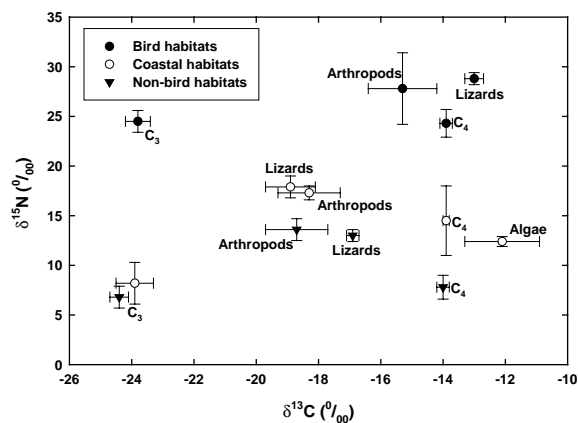


Fig. 1. The relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for communities in inland seabird-dominated areas, coastal areas without seabirds, and inland areas without seabirds on islands and the mainland coast in the Midriff region of Baja California, Mexico.

Uta stansburiana, in the Gulf of California have diets that are subsidized by the marine system. We used the stable isotopes of C and N to demonstrate empirically that marine materials in lizard diets are transferred to islands from both tidal action and seabirds. We also demonstrated that lizards in marine subsidized habitats are more abundant than in unsubsidized areas.

Elevated $\delta^{15}\text{N}$ values of lizards in inland seabird habitats indicate these populations are consuming arthropods subsidized by marine material brought to the island by seabirds (Fig. 1). Seabird material is incorporated into arthropod communities either directly as they parasitize seabirds or feed on their carcasses, or indirectly as herbivores and detritivores feed on plants fertilized by guano (Sanchez-Piñero and Polis 2000).

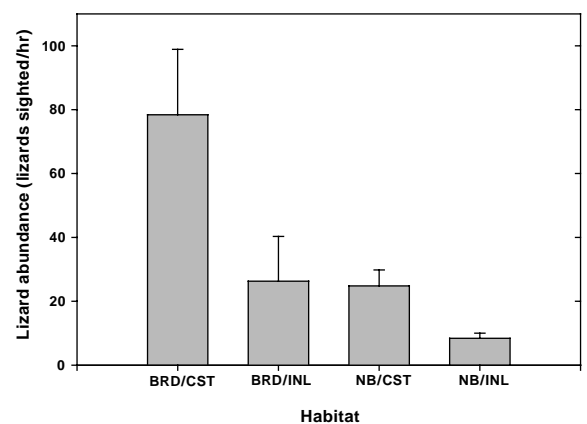


Fig. 2. Mean lizard abundance and standard error from four habitats on 18 islands and the mainland coast in the Midriff region of Baja California, Mexico. Lizards on Bird islands and in coastal areas were significantly more abundant than lizards on Non-bird islands and in inland areas, respectively (Table 3). BRD/CST = coastal areas of Bird islands; BRD/INL = inland areas of Bird islands; NB/CST = coastal areas of Non-bird islands; NB/INL = inland areas of Non-bird islands.

Table 3. ANOVA table for the analysis of lizard density as a function of seabird presence and island location (coast or inland).

Source	df	SS	MS	F	p
Island type (bird/non-bird)	1	1.39	1.39	4.84	0.04
Error-main plots	16	4.6	0.29		
Island location (coast/inland)	1	2.97	2.97	27.66	<0.0005
Type × location	1	0.04	0.04	0.38	0.55
Error-subplots	16	1.72	0.11		
Total	35	10.71			

Because guano $\delta^{15}\text{N}$ values are much higher than seabird tissues (Wainright et al. 1998), the very high $\delta^{15}\text{N}$ values of lizards on islands with seabirds indicates that the guano → plant → herbivore pathway subsidizes lizards rather than a pathway where lizards consume arthropods that feed on seabird carcasses. Known seabird ectoparasites (which also feed on guano) had $\delta^{15}\text{N}$ values far above even the highest $\delta^{15}\text{N}$ values of lizards on seabird islands (38.1‰ and 28.8‰, respectively); therefore, *U. stansburiana* are not likely consuming these ectoparasites in large quantities. Lizards on islands with seabirds also had $\delta^{13}\text{C}$ values that were significantly different from populations in the other habitat types. Such a result most likely occurs because guano deposition by seabirds increases the dominance of C_4 plants (W. B. Anderson and D. A. Wait, unpubl.).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from sampled organisms also demonstrated the importance of marine materials washed ashore by tides. Results from a two-end-member mixing model demonstrated that, on average, 40% of a lizard's diet in coastal areas is based on arthropods that have consumed algae. $\delta^{15}\text{N}$ values for coastal populations of *U. stansburiana* differed from values for unsubsidized inland populations and populations on the interior of islands with seabirds. Lizard populations in coastal habitats had lower $\delta^{15}\text{N}$ values than those lizards from the interior of seabird islands, indicating that inputs from seabirds are minimal in the coastal habitats sampled. The significantly greater $\delta^{15}\text{N}$ values of lizards in coastal areas relative to populations in unsubsidized inland areas partially results from the relatively high $\delta^{15}\text{N}$ values of algae compared to inland plants on Non-bird islands.

An additional explanation for the elevated $\delta^{15}\text{N}$ value of lizard populations in coastal habitats relative to unsubsidized inland populations may lie in the increased number of trophic positions found in subsidized food webs. Polis and Strong (1996) point out that the reticulate connections that exist in most food webs may become especially complicated in spatially subsidized and/or highly productive systems (Schoener 1989, Polis and Hurd 1996b). If the spatially subsidized coast has an additional trophic link that is absent in the unsubsidized inland areas, then lizards would be expected to exhibit slightly higher $\delta^{15}\text{N}$ values compared to their inland counterparts (controlling for basal

$\delta^{15}\text{N}$ values; Post 2002). This supposition is supported by the significantly higher trophic position of coastal lizard populations relative to unsubsidized inland populations.

Previous studies have noted strong relationships between the density of certain consumer groups and spatial subsidies from tidal action and/or seabirds (Polis and Hurd 1995, 1996a, Sanchez-Piñero and Polis 2000). We detected a similar relationship with lizards on several islands in the Gulf (Fig. 2). The greatest median abundance was found on the coast of Bird islands. Here lizards have access to marine subsidies from both the seabird and tidal conduit. Thus, while we did not have access to such habitat for our diet study, results reported here strongly suggest lizards are consuming both types of marine subsidies in these locations.

We found no relationship between island size and lizard abundance. This finding for lizards is in contrast with results from spider (Polis and Hurd 1995) and rodent (Stapp and Polis 2003) studies in this region. These studies found smaller islands to have higher consumer densities because they receive proportionately greater marine material via tidal action. Some unmeasured effect of predation or competition may help to explain our results.

In conclusion, this study provides the first demonstration of a marine-to-terrestrial connection resulting from both coastal and seabird inputs to lizards (secondary consumers). The patterns described here are similar to those found for lizards in riparian habitats, which are linked to streams (Sabo and Power 2002). Our longterm survey data imply that subsidies can greatly increase lizard abundance. This result is supported by the work of Markwell and Daugherty (2002), who found increased lizard density in areas of seabird activity on islands near New Zealand. The impact of spatial subsidies on the diet and population and community dynamics of many organisms may be far reaching (Polis et al. 1997). Because all habitats are a mosaic of smaller patches, often with differential productivity, understanding the effect of energy transfer among patches has implications beyond this system.

Acknowledgements – We would like to thank Brian D. Green, the Guyer Lab at Auburn University, Lauri Oksanen, and Shannon Barrett for comments on an earlier version of the manuscript. Doug Aubrey, Shannon Barrett, Kate Heckman, Caleb Hickman, Jessica Rowe, Matt Stone and many Mexican

boatmen assisted in the field, along with a host of undergraduates from Drury University and Southwest Missouri State University. John S. Heywood offered statistical advice. Funding was provided by Southwest Missouri State University (Department of Biology, Graduate College, Boritski Scholarship) and Sigma Xi, through a Grants-in-Aid of Research (K.B.). We thank the Mexican Department of the Environment for a permit to work on the islands (SEMARNAT #1448).

References

- Anderson, W. B. and Polis, G. A. 1998. Marine subsidies of island communities in the Gulf of California: evidence from stable carbon and nitrogen isotopes. – *Oikos* 81: 75–80.
- Anderson, W. B. and Polis, G. A. 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. – *Oecologia* 118: 324–332.
- Anderson, W. B. and Wait, D. A. 2004. Allochthonous nutrient and food inputs: consequences for temporal stability. – In: Polis, G. A., Power, M. E. and Huxel, G. R. (eds), *Food webs at the landscape scale*. Univ. of Chicago Press, pp. 82–114.
- Bouchard, S. S. and Bjorndal, K. A. 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. – *Ecology* 81: 2305–2313.
- Doughty, P., Sinervo, B. and Burghardt, G. M. 1994. Sex-biased dispersal in a polygynous lizard, *Uta stansburiana*. – *Anim. Behav.* 47: 227–229.
- Felger, R. S. and Lowe, C. S. 1976. The island and coastal vegetation and flora of the northern part of the Gulf of California. – *Contrib. Sci. Nat. Hist. Mus. Los Angeles* 285: 1–31.
- Gannes, L. Z., O'Brian, D. M. and del Rio, C. M. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. – *Ecology* 78: 1271–1276.
- Gasith, A. and Hasler, A. D. 1976. Airborne litterfall as a source of organic matter in lakes. – *Limnol. Oceanogr.* 21: 253–258.
- Gastil, G., Minch, J. and Phillips, R. P. 1983. The geology and ages of the islands. – In: Case, T. J. and Cody, M. L. (eds), *Island biogeography in the Sea of Cortez*. Univ. of California Press, pp. 13–25.
- Hesslein, R. H., Capel, M. J., Fox, D. E. et al. 1991. Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the Lower Mackenzie River Basin, Canada. – *Can. J. Fish. Aquat. Sci.* 48: 2258–2265.
- Hilderbrand, G. V., Hanley, T. A., Robbins, C. T. et al. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. – *Oecologia* 121: 546–550.
- Hutchinson, G. E. 1950. The biogeochemistry of vertebrate excretion. – In: *Survey of existing knowledge of biogeochemistry*. Bull. Am. Mus. Nat. Hist. 96.
- Huxel, G. R. and McCann, K. 1998. Food web stability: the influence of trophic flows across habitats. – *Am. Nat.* 152: 460–469.
- Jansson, M., Bergstrom, A., Blomqvist, P. et al. 2000. Allochthonous organic carbon and phytoplankton/bacterioplankton production relationships in lakes. – *Ecology* 81: 3250–3255.
- Lindeboom, H. J. 1984. The nitrogen pathway in a penguin rookery. – *Ecology* 65: 269–277.
- Magnuson, W. E., Lima, A. P., Faria, A. S. et al. 2001. Size and carbon acquisition in lizards from Amazonian savannah: evidence from stable isotopes. – *Ecology* 82: 1772–1780.
- Markwell, T. J. and Daugherty, C. H. 2002. Invertebrate and lizard abundance is greater on seabird-inhabited islands than on seabird-free islands in the Marlborough Sounds, New Zealand. – *Ecoscience* 9: 293–299.
- Maulf, L. Y. 1983. The physical oceanography. – In: Case, T. J. and Cody, M. L. (eds), *Island biogeography in the Sea of Cortez*. Univ. of California Press, pp. 26–45.
- Murphy, R. W., Sanchez-Piñero, F., Polis, G. A. et al. 2002. New measurements of area and distance for islands in the Sea of Cortez. – In: Case, T. J., Cody, M. L. and Ezcurra, E. (eds), *A New Island biogeography in the Sea of Cortez*. Oxford Univ. Press, pp. 447–464.
- Nakano, S., Miyasaka, H. and Kuhara, N. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. – *Ecology* 80: 2435–2441.
- Peterson, B. J., Howarth, R. W. and Garritt, R. H. 1985. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. – *Science* 227: 1361–1363.
- Polis, G. A. and Hurd, S. D. 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. – *Proc. Natl. Acad. Sci. USA* 92: 4382–4386.
- Polis, G. A. and Hurd, S. D. 1996a. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. – *Am. Nat.* 147: 396–423.
- Polis, G. A. and Hurd, S. D. 1996b. Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: examples from the ocean-land interface. – In: Polis, G. A. and Winemiller, K. O. (eds), *Food webs: integration of patterns and dynamics*. Chapman and Hall, pp. 275–285.
- Polis, G. A. and Strong, D. A. 1996. Food web complexity and community dynamics. – *Am. Nat.* 47: 813–846.
- Polis, G. A., Anderson, W. B. and Holt, R. D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. – *Ann. Rev. Ecol. Syst.* 28: 289–316.
- Ponsard, S. and Averbuch, P. 1999. Should growing and adult animals fed on the same diet show different $\delta^{15}\text{N}$ values? – *Rapid Comm. Mass Spectrom.* 13: 1305–1310.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. – *Ecology* 83: 703–718.
- Reyes-Coca, S., Miranda-Reyes, F. and Garcia-Lopez, J. 1990. *Climatología de la region noroeste de Mexico. I. Precipitación*. Publication EBA no 3. Centro de Investigacion Científica y Educacion Superior de Enseada, Ensenada, Mexico.
- Sabo, J. L. and Power, M. E. 2002. River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. – *Ecology* 83: 1860–1869.
- Sanchez-Piñero, F. and Polis, G. A. 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. – *Ecology* 81: 3117–3132.
- Schoener, T. W. 1989. Food webs from the small to the large. – *Ecology* 70: 1559–1589.
- Sobey, D. G. and Kenworthy, J. B. 1979. The relationship between herring gulls and the vegetation of their breeding colonies. – *J. Ecol.* 67: 469–496.
- Stapp, P. and Polis, G. A. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. – *Oecologia* 134: 496–504.
- Stapp, P., Polis, G. A. and Sanchez-Piñero, F. 1999. Stable isotopes reveal strong marine and El Niño effects on island food webs. – *Nature* 401: 467–469.
- Tinkle, D. W. 1967. The life and demography of the side-blotched lizard, *Uta stansburiana*. – *Mus. Zool., Univ. of Michigan*, No. 132, pp. 90–100.
- Wainright, S. C., Haney, J. C., Kerr, C. et al. 1998. Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. – *Mar. Biol.* 131: 63–71.
- Wait, D. A., Aubrey, D. P., and Anderson, W. B. 2004. Seabird guano influences on desert islands: soil chemistry and

- herbaceous species richness and productivity. – *J. Arid Environ.* 60: 681–695.
- Welcomme, R. 1979. Fisheries ecology of floodplain rivers. – Longmans.
- Wiens, J. A. 1992. Ecological flows across landscape boundaries: a conceptual overview. – In: di Castri, F. and Hansen, A. J. (eds), Landscape boundaries. Springer-Verlag, pp. 216–235.
- Wolf, B. O., del Rio, C. M. and Babson, J. 2002. Stable isotopes reveal that saguaro fruit provides different resources to two desert dove species. – *Ecology* 83: 1286–1293.

Appendix A

Stable isotope techniques

We calculated stable isotope values by comparing the stable isotope ratio of either carbon (C) or nitrogen (N) in a sample to the stable isotope ratio of C or N in a standard. The standards for C and N isotopes were Pee Dee Belemnite carbonate and atmospheric N₂, respectively (Peterson and Fry 1987). The isotopic value of an element (δX) is essentially a ratio of ratios, is expressed on a “per mil” basis, and was formulated as:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000\%$$

here X is the relative concentration of the heavier isotope (e.g. ¹³C or ¹⁵N), R_{sample} is the isotopic ratio in the sample, and R_{standard} is the isotopic ratio in the standard (Boutton 1991).

The generic two-end-member mixing model used was:

$$\delta^{13}C_{\text{lizards}} = p(\delta^{13}C_X) + (1 - p)(\delta^{13}C_Y) + \Delta$$

where p is the proportion of material derived from source X, and $\delta^{13}C_{\text{lizards}}$, $\delta^{13}C_X$, and $\delta^{13}C_Y$ are the isotope compositions of *U. stansburiana*, possible C source X, and possible C source Y, respectively. Δ represents the predicted ¹³C enrichment or the consumer relative to the prey item (0.3‰ per trophic level, Post 2002). We also estimated the maximum and minimum possible values for the two-end-member mixing model by using the appropriate combination of maximum and minimum focal and alternate carbon sources available to lizards.

For inland lizards on Non-bird islands with access to resources from only one food web, we used the following model to estimate trophic position:

Trophic position

$$= \lambda + (\delta^{15}N_{\text{secondary consumer}} - \delta^{15}N_{\text{base}})/\Delta_n$$

where λ is the trophic position of the organism used to estimate $\delta^{15}N_{\text{base}}$. We considered the base of the food web for inland areas of Non-bird islands to be terrestrial C₃ and C₄ plants, all of which had very similar $\delta^{15}N$ values (Table 2). We measured $\delta^{15}N_{\text{secondary consumer}}$ directly, and Δ_n is the enrichment of $\delta^{15}N$ per trophic level (3.4‰, Peterson and Fry 1987, Post 2002).

For coastal populations of *U. stansburiana* with access to resources from two food webs (i.e. coastal and terrestrial), trophic position was calculated following the model reviewed in Post (2002):

$$\text{Trophic position} = \lambda + (\delta^{15}N_{\text{secondary consumer}} - [\delta^{15}N_{\text{base1}} \times \alpha + \delta^{15}N_{\text{base2}} \times (1 - \alpha)])/\Delta_n$$

where α is the proportion of N in the consumer ultimately derived from the base of food web one. α was estimated using carbon isotopes as follows:

$$\alpha = (\delta^{13}C_{\text{secondary consumer}} - \delta^{13}C_{\text{base1}})/(\delta^{13}C_{\text{base1}} - \delta^{13}C_{\text{base2}})$$

We collected tissue samples during the periods of March 11–16, 2001, May 17–June 3, 2001 and March 10–14, 2002. We collected plant samples (leaf material) from inland areas of Non-bird islands, inland areas of Bird islands, and coastal habitats on Non-bird islands and dried them in an oven to preserve them until they could be returned to the lab and processed. We collected arthropods and lizards from the three habitats listed above primarily by hand, although we inadvertently collected a few specimens of each type in pitfall traps haphazardly placed in the designated habitat types for an unrelated experiment. We used whole arthropods so we could homogenize the entire organism for isotope analysis. We used tail tissues for the stable isotope analysis of lizards. After we captured a lizard, we removed no more than approximately 10 mm of the tail and then released the lizard at the point of capture. We preserved animal samples by freezing them until they could be returned to the lab for processing. We expected homogenized arthropod bodies and tail samples to yield diet information reflecting a mixture of long- and short-term diet (weeks to months; Tieszen and Boutton 1989). Samples were prepared for analysis by weighing approximately 0.1 mg of animal material and 2.0 mg of plant material into 9 × 5 mm tin cups. We sent prepared samples to the University of Arkansas Stable Isotope Laboratory for analysis. Stable isotope content of the samples were analyzed using a CE Instruments NC2500 elemental analyzer connected to a Finnigan Delta Plus stable isotope mass spectrometer. The precision was greater than 0.2‰ for C and 0.4‰ for N.

References

- Boutton, T. W. 1991. Stable carbon isotope ratios of natural materials: I. Sample preparation and mass spectrometric analysis. – In: Coleman, D. C. and Fry, B. (eds), Carbon isotope techniques. Academic Press, pp. 155–172.

- Peterson, B. J. and Fry, B. 1987. Stable isotopes in ecosystem studies. – *Annu. Rev. Ecol. Syst.* 18: 293–320.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. – *Ecology* 83: 703-718.
- Tieszen, L. L. and Boutton, T. W. 1989. Stable isotopes in terrestrial ecology. – In: Rundel, P. W., Ehleringer, J. R. and Nagy, K. A. (eds), *Stable isotopes in ecological research*. Springer-Verlag, pp. 164–195.