

# Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies

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**Abstract.** Adjacent food webs may be linked by cross-boundary subsidies: more-productive donor systems can subsidize consumers in less-productive neighboring recipient systems. Introduced species are known to have direct effects on organisms within invaded communities. However, few studies have addressed the indirect effects of nonnative species in donor systems on organisms in recipient systems. We studied the direct role of introduced trout in altering a lake-derived resource subsidy and their indirect effects in altering a passerine bird's response to that subsidy. We compared the abundance of aquatic insects and foraging Gray-crowned Rosy-Finches (*Leucosticte tephrocotis dawsoni*, "Rosy-Finch") at fish-containing vs. fishless lakes in the Sierra Nevada Mountains of California (USA). Introduced trout outcompeted Rosy-Finches for emerging aquatic insects (i.e., mayflies). Fish-containing lakes had 98% fewer mayflies than did fishless lakes. In lakes without fish, Rosy-Finches showed an aggregative response to emerging aquatic insects with 5.9 times more Rosy-Finches at fishless lakes than at fish-containing lakes. Therefore, the introduction of nonnative fish into the donor system reduced both the magnitude of the resource subsidy and the strength of cross-boundary trophic interactions. Importantly, the timing of the subsidy occurs when Rosy-Finches feed their young. If Rosy-Finches rely on aquatic-insect subsidies to fledge their young, reductions in the subsidy by introduced trout may have decreased Rosy-Finch abundances from historic levels. We recommend that terrestrial recipients of aquatic subsidies be included in conservation and restoration plans for ecosystems with alpine lakes.

**Key words:** aquatic-insect emergence; aquatic-terrestrial linkages; *Callibaetis ferrugineus*; density-mediated indirect effect; ecosystem boundary; ecosystem subsidy; fish stocking; food web; land–water interface; *Oncorhynchus mykiss*; *Passeriformes*; *Salvelinus fontinalis*.

## INTRODUCTION

Ecological boundaries such as the interface between terrestrial and aquatic ecosystems mark a division between habitat types. Such boundaries, however, frequently are not barriers to the flow of energy between neighboring habitats. Rather, cross-boundary resource fluxes can have positive effects on the recipient community (e.g., Polis et al. 1997, Marczak et al. 2007). For example, aquatic-resource subsidies can strongly influence a wide range of terrestrial consumers, including invertebrates (Kato et al. 2003, Paetzold et al. 2005), lizards (Sabo and Power 2002), and birds (Zaret and Paine 1973, Gray 1993, Gende and Willson 2001, Nakano and Murakami 2001). This is often studied in the context of a more-productive donor ecosystem that subsidizes consumers in an adjacent and less-productive

recipient ecosystem (Polis and Hurd 1996, Winemiller and Jepsen 2004).

Although introduced predators can have indirect effects on organisms within invaded communities (e.g., Hurlbert et al. 1986, Schoener et al. 2002, Townsend 2003), the indirect effects of nonnative species in donor ecosystems on recipient ecosystems have only recently been addressed (Baxter et al. 2004, Maron et al. 2006, Finlay and Vredenburg 2007). Whether or not predators in the donor community are native, they are likely to alter nutrient transfer (Schindler et al. 2001, Simon et al. 2004). Consequently, these predators are likely to reduce both trophic efficiency and nutrient export (i.e., a subsidy) from the donor system to consumers in the recipient system (Baxter et al. 2004). Therefore, the introduction of predators into the donor community may reduce the magnitude of a resource subsidy and the strength of cross-boundary trophic interactions (Pace et al. 1999, Knight et al. 2005). In this study, we quantified the effect of an introduced predator in the donor system on spatial aggregation of subsidy consumers in the recipient system.

Mountain ecosystems often contain high densities of lakes, habitats created following the retreat of glaciers at

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the end of the Pleistocene epoch ~12000 years ago. Most of these lakes were naturally fishless, but have since been stocked with fish in an effort to create recreational fisheries (Knapp et al. 2001a, Pister 2001, Schindler and Parker 2002, Denoel et al. 2005). In California's Sierra Nevada (USA), nonnative salmonids have been introduced to the majority of the thousands of naturally fishless lakes (Knapp 1996, Knapp et al. 2001b, 2005). As such, this system provides an excellent opportunity to investigate interactions between native and nonnative species in donor aquatic ecosystems and their effects on birds in the adjacent recipient terrestrial ecosystems. Previous food web studies in the Sierra Nevada have shown strong direct and indirect effects of nonnative fish on lentic communities (Bradford et al. 1993, Knapp and Matthews 2000, Knapp et al. 2001b, 2005, Vredenburg 2004, Finlay and Vredenburg 2007), but their ecological impacts on adjacent terrestrial ecosystems are unknown.

The Sierra Nevada alpine habitat is a harsh environment generally characterized by limited food resources. Thus, aquatic subsidies may provide an important resource for terrestrial consumers. Alpine lakes are oligotrophic environments that experience short growing seasons and low productivity (Schindler et al. 2001, Sarnelle and Knapp 2005). Similarly, the recipient terrestrial habitats have low primary productivity (Billings and Mooney 1968). However, the annual, synchronous flux of thousands of adult mayflies (*Callibaetis ferrugineus* and *Ameletus edmundsi*) emerging from a single alpine fishless lake (millions per lake basin) creates a strong but ephemeral productivity gradient between the aquatic and terrestrial habitats. This productivity gradient spans a two-week period over which the mayfly emergence takes place. In Sierra Nevada alpine lakes mayflies constitute a large biomass (agglomerate and per capita measures) relative to other common aquatic invertebrates such as chironomids (Finlay and Vredenburg 2007). Therefore, the flow of energy from donor alpine lentic systems to recipient terrestrial systems is primarily in the form of mayflies.

The introduction of fish to mountain lakes generally results in the extinction or severe reduction of mayfly populations (Luecke 1990, Knapp et al. 2001b, Caudill 2003, Finlay and Vredenburg 2007). Consequently, impacts of aquatic subsidies are predicted to be strong at the interface between fishless lakes and terrestrial uplands, and weak between fish-containing lakes and the surrounding uplands (Finlay and Vredenburg 2007). Fishless lakes should provide a greater insect prey base that can be exploited by alpine predators, particularly generalist consumers. We examined the role of introduced trout in altering the abundance of a lake-derived insect subsidy and the resulting effects on the Gray-crowned Rosy-Finch (*Leucosticte tephrocotis dawsoni*, hereafter "Rosy-Finch"), a passerine bird that utilizes this subsidy.

We focused this study on the Rosy-Finch for several reasons. Rosy-Finches are one of only a few bird species that nest in alpine regions of the Sierra Nevada. They are wide-ranging, omnivorous, non-territorial, central-place foragers that opportunistically and communally feed on seeds and insects, including adult mayflies (Twining 1940, Miller 1988). When mayflies are available, they may comprise as much as 38% of the Rosy-Finch diet (Epanchin 2009). During the breeding season, Rosy-Finches primarily feed their young a diet of insects (Grinnell and Storer 1924, Twining 1938, Miller 1988, Epanchin 2009). As suggested by Francis et al. (2006), if the timing of the subsidy coincides with important life history events of a consumer, such as the provisioning of nestlings or fledglings, then the consumer is likely to respond to the subsidy.

Here we tested the prediction that introduced trout indirectly affect the Rosy-Finches' aggregative response to mayfly prey, via exploitative competition for different life stages of the same insects (i.e., aquatic nymphs and terrestrial adults; Fig. 1). We predicted that fish presence in a lake negatively affects mayfly abundance and that Rosy-Finch foraging activity at a lake is directly related to mayfly emergence and therefore indirectly related to fish presence. This would result in more Rosy-Finches at fishless lakes than at fish-containing lakes, particularly during periods of mayfly emergence when adult mayfly densities are highest.

## METHODS

### *Study area and design*

We conducted the study in five headwater lake basins in the southern Sierra Nevada (Appendix A; see Plate 1). Mayfly and Rosy-Finch data collection occurred during June–August at four lakes in 2004, eight lakes in 2005, and 24 lakes in 2006. In 2004, we sampled four lakes in Humphreys Basin (John Muir Wilderness, hereafter "JMW," Sierra National Forest). In the subsequent two years of the study (2005 and 2006), we sampled these four lakes and two others in Humphreys Basin. In 2005, in addition to the six lakes in Humphreys Basin, we sampled two others in the adjacent French Canyon. In 2006, we tested the generality of our predictions by expanding the study to encompass 24 lakes within four headwater lake basins. In addition to the six lakes in Humphreys Basin, we sampled six lakes in Pinnacles Basin (JMW, Sierra National Forest), four lakes in Big Pine Basin (JMW, Inyo National Forest), and eight lakes in Sixty Lake Basin (Kings Canyon National Park). To increase survey efficiency, we did not include the two French Canyon lakes in our 2006 survey. The entire study area was ~60 km (north–south) by 20 km (west–east; Appendix A).

In each year we compared the biota at paired fish-containing and fishless lakes. We used a randomized complete design with paired lakes as replicates. Each replicate consisted of a fishless lake and a nearby fish-containing lake in the same basin (Appendix A). Fishless

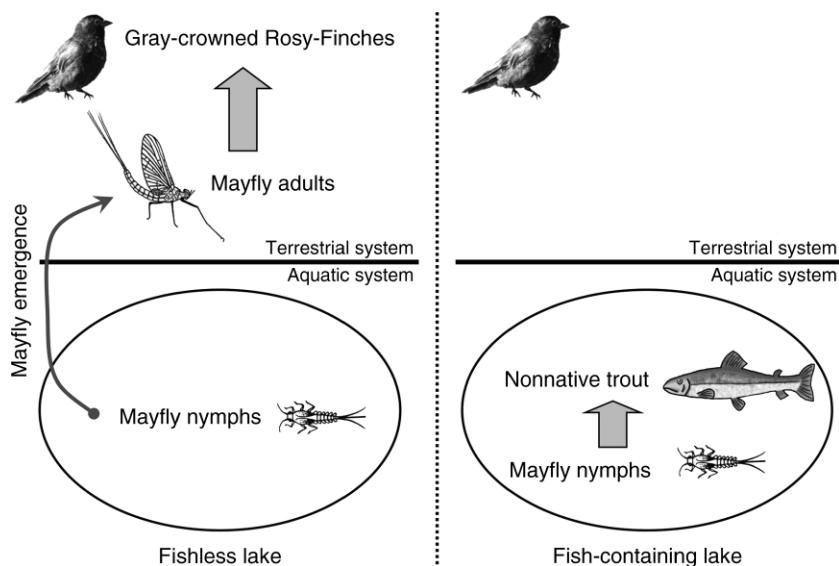


FIG. 1. Conceptual model of the movement of resources originating in an alpine fishless lake (left) and fish-containing lake (right). On the left, mayfly nymphs emerge from a fishless lake into a terrestrial system, thus supplementing the diet of an avian predator. On the right, the population of mayfly nymphs is intensively preyed upon by nonnative fish. This substantially diminishes or eliminates the movement of aquatic resources to avian recipients, thereby severing trophic linkages between the terrestrial and aquatic systems.

lakes either were never stocked ( $n = 7$ ) or had their fish removed between 1997 and 2000 ( $n = 6$ ) (Milliron 2001, Vredenburg 2004, Sarnelle and Knapp 2005). The status of fish in each lake was based on surveys conducted from 1995 to 1997 (Knapp and Matthews 2000, Milliron 2001, Knapp et al. 2003); in these five study basins trout currently occupy 83% of the surface area of lakes and ponds. To control for environmental heterogeneity, lake pairs were chosen to minimize differences in elevation, between-lake distances, lake depth, and surface area. To control for weather, we simultaneously sampled paired lakes. The fish species in our study lakes were golden trout (*Oncorhynchus mykiss aguabonita*)  $\times$  rainbow trout (*O. mykiss*) hybrids and brook trout (*Salvelinus fontinalis*). Based on lake depth, all study lakes were capable of supporting trout (Knapp and Matthews 2000).

#### Aquatic-insect sampling

At each lake, we measured insect emergence with four emergence traps anchored in the littoral zone at each cardinal direction. Nymphs of both mayfly species are restricted to the littoral zone (Edmunds et al. 1976). Traps were hemispherical, floated on the lake surface, and were covered with a polyester mesh ( $\sim 0.75$ -mm mesh size) with a closable sleeve used to access the inside of the trap (Appendix B). Each trap covered a surface area of  $0.25 \text{ m}^2$ . Traps were set at each lake every 1–2 weeks for a 24-h period, during which a 2-h avian point count was conducted (see *Bird surveys*). Traps were set  $\sim 20$  h prior to the point count and were removed 2 h after the point count. Prior to trap removal, insects were collected with an aspirator and preserved in 70% ethyl alcohol. Emergent insects were identified to family,

genus, or species under a dissecting microscope (7.5–75 $\times$ ).

For each year, we categorized each insect sampling date as either before, during, or after the 2–3 week mayfly-emergence period. The during-emergence period was defined as  $\geq 1$  mayfly trapped or seen. We used a low number of mayflies to define the emergence period because our traps covered a small area of each lake. As a result, even a small number of trapped mayflies can scale up to represent a large emergence. Mayflies were typically absent from fish-containing lakes. Therefore, the categorization (before, during, or after mayfly emergence) of insect sampling dates at each fish-containing lake was based on that developed for its paired fishless counterpart; emergences tend to be synchronous among lakes of similar elevation.

Prior to the 2006 mayfly emergence, we sampled the benthic macroinvertebrate community in the littoral zone at each of the 24 lakes surveyed that year. In each lake we sampled a total of  $4.5 \text{ m}^2$  of the littoral benthos with 15 standard sweeps of a D-net (0.5-mm mesh size; Knapp et al. 2001b). In approximate proportion to their occurrence, we sampled littoral substrates within 0–2 m of the shoreline, in water  $\leq 1.2$  m deep. We preserved macroinvertebrates in 70% ethyl alcohol, used a dissecting microscope (7.5–75 $\times$ ) to identify them to family, genus, or species (Merritt and Cummins 1996), and counted them. We only counted mature mayfly nymphs  $>0.5$  cm in length (those likely to have emerged in the following weeks). We counted all size classes of other common benthic macroinvertebrates.

Using all 24 lakes in the four lake basins sampled in 2006 we estimated the total production of mayflies



PLATE 1. A fishless study lake as seen from the inlet, Knob Lake (3.4 ha) in the Humphreys Basin, John Muir Wilderness Area, Sierra National Forest, California, USA. Photo credit: P. N. Epanchin.

(mean density  $\pm$  standard error] of mayfly nymphs per square meter of littoral zone in each lake type) under two scenarios: the historic fishless condition of all lakes, and the present condition of a mix of both fishless and fish-containing lakes. We then estimated the percentage of decline in mayfly productivity between the historic and current scenarios. Using lake perimeters we calculated the area of the littoral zone for all lakes and ponds  $\geq 2$  m deep in each of the four study basins. A water depth of 2 m protects lakes from complete winter freezing and summer drying (Knapp and Matthews 2000, Lacan et al. 2008). We conservatively limited our estimate of the extent of the littoral zone to the area sampled with D-nets: 0–2 m from the shoreline. We estimated basin-wide mayfly densities by multiplying the mean number of mayfly nymphs per square meter for each lake type by the total area of fish-containing or fishless littoral zone under historic and present conditions. Using one standard error from the calculated total number of mayflies produced under both scenarios, we estimated an upper and lower level of total mayfly production. We used this error to describe the sensitivity of the estimated decline in mayfly production to variability in mayfly density. A minimum decline was estimated using the percentage of decline from the current level of mayfly production plus one standard error, to the historic level of mayfly production minus one standard error, and vice versa for a maximum decline.

#### *Bird surveys*

We counted Rosy-Finches at each lake every 1–2 weeks during their breeding season. At each of the paired lakes, we conducted simultaneous point counts of foraging birds using binoculars (10 $\times$ ) from 08:30 to 10:30 (the peak time of mayfly emergence; Twining 1940; P. Epanchin, *personal observation*). This time period was split into 12 consecutive 10-min blocks. We recorded the total number of birds at the lake during each block and from this calculated a daily mean number of Rosy-Finches per lake. Each avian-survey day was categorized as before, during, or after mayfly emergence based on the concurrent insect sample for that lake pair. Several point counts were typically conducted at each lake during each stage of mayfly emergence; however, in some years some lakes were not visited before or after the mayfly emergence and thus we had an unbalanced design. The before-mayfly emergence period was not surveyed in 2004. At each lake, point counts within the same mayfly emergence time period were treated as subsamples. Thus, the number of Rosy-Finches was averaged within each category of mayfly emergence and the average was used in subsequent analyses. Sample effort in each of the three years were as follows: 68 observer-hours at four lakes in 2004 (mean observer-hours per lake = 17); 94 observer-hours at 8 lakes in 2005 (mean observer-hours per lake = 12); and 242 observer-hours at 24 lakes in 2006 (mean observer-hours per lake = 10).

### *Analytical methods*

All analyses were conducted using SAS 9.1 (SAS Institute 2002). Unless otherwise stated, we used a significance criterion of  $P < 0.05$ . Prior to analyzing whether the distribution of either aquatic invertebrates or Rosy-Finches was related to fish presence, we tested whether underlying habitat attributes associated with the study lakes (i.e., tree density, lake surface elevation, lake depth, lake perimeter, lake surface area, and the ratio of perimeter to surface area) varied with fish presence. To test this we ran 41 logistic regression models (PROC LOGISTIC) using all combinations of up to three habitat variables as additive effects. Given our relatively small sample sizes, we assumed that including more than three habitat variables would weaken model fit. In addition, we tested for possible quadratic relationships by running an additional logistic regression model for each habitat variable; models included a linear and quadratic term. In all models we evaluated variable significance, but selected the best-fitting model using Akaike's information criteria, adjusted for small sample size ( $AIC_c$ ). Lake surface elevation, lake perimeter, and lake surface area were acquired from 7.5-minute U.S. Geological Survey topographic maps. Lake depths were measured in previous studies (Knapp and Matthews 2000, Milliron 2001, Knapp et al. 2003). Tree density was sampled at each lake (in 2006) using four  $25 \times 10$  m belt transects placed perpendicular to the shore at each cardinal direction, and the number of trees  $\geq 1.5$  m tall within each transect was recorded.

To test for differences in aquatic invertebrate density between lake types, we calculated the 2006 mean density (individuals per square meter) of the most common littoral-dwelling aquatic invertebrate taxa for each lake and compared densities of invertebrate taxa between the 12 fishless and the 12 fish-containing lakes using a Wilcoxon-Mann-Whitney two-sample test (PROC NPAR1WAY). We used the Bonferroni method to correct for having run multiple tests. We used a multiple linear regression analysis (PROC REG) to test whether differences in prey (i.e., mayfly) density between lakes were best explained by fish presence or by habitat variables. We ran 42 models with fish presence as the predictor variable and tested all combinations of up to three physical habitat parameters (i.e., covariates).  $AIC_c$  was used to select the best-fitting model.

We used a multiple linear regression analysis (PROC GLM) to explicitly test the relationship between the number of collected mayfly nymphs (predictor variable) at a lake and the mean number of foraging Rosy-Finches (response variable) observed at the same lake during the mayfly emergence time period, irrespective of fish presence. To address possible confounding effects of other factors that may influence Rosy-Finch abundances at lakes, we used the paired design in the analysis and included the six habitat covariates in the models. We ran 42 models, each model with the predictor variable (i.e.,

the number of mayfly nymphs), lake pair, and all combinations of up to three covariates.  $AIC_c$  was used to select the best-fitting model. To meet model assumptions, we log-transformed ( $\log(1 + Y)$ ) the predictor and response variables.

To test for an aggregative response of Rosy-Finches to changes in the availability of mayfly prey over time, we used a general linear mixed-effects model (PROC MIXED) to compare the mean Rosy-Finch response between lake type (fishless or fish-containing) across the three mayfly emergence periods (before, during, and after). This was a repeated-measures design where the repeated measure was the mean number of Rosy-Finches observed in each mayfly emergence period at each lake and across years. We treated lake type and time as fixed factors and lake-pair as a random factor. We ran 42 models, each model with the two predictor variables (i.e., lake type and mayfly emergence period), lake pair, and combinations of up to three of the six covariates. We used standard variance components for the covariance structure of the **R** matrix. For a more accurate  $P$  value, we computed the  $F$  statistic with a general Satterthwaite approximation of the denominator degrees of freedom (West et al. 2007). We used  $AIC_c$  to select the best-fitting model.

We compared the number of Rosy-Finches between the two lake types within each mayfly emergence period using differences of least-square means from the best-fitting general linear effects model for the mayfly emergence period  $\times$  lake type interaction. Because data were not collected before the mayfly emergence in 2004, we only used data from 2005 and 2006 to analyze the Rosy-Finch response at the "before-emergence" time period. We used a separate mixed-effects model that incorporated data from all three years to analyze the "during" and "after" mayfly-emergence time periods. To account for testing the Rosy-Finch response at three stages of the mayfly emergence, we applied a Bonferroni adjustment to least-square means comparisons.

## RESULTS

### *Distribution of fish and aquatic insects*

None of the measured limnological or terrestrial habitat variables were significantly associated with fish presence-absence in the models examined. The best-fitting logistic regression model included only lake perimeter as an additive predictor of fish presence (Appendix C), but this variable was not significant ( $n = 26$ , odds ratio = 1.001,  $P = 0.23$ ).

Mayfly density was negatively related to fish presence and positively related to tree density, as per the best-fitting multiple regression model (Appendix D). Fish presence was a significant predictor of mayflies in all models. Tree density reached the level of statistical significance only in the best-fitting model. Other habitat variables were not significant predictors of mayfly density in any model.

Based on the 2006 D-net samples, fish-containing lakes had 98% fewer mayfly nymphs than fishless lakes, (Wilcoxon-Mann-Whitney two-sample test  $Z = -4.1358$ ,  $P < 0.0001$ ). Littoral mayfly nymph density was 46.3 nymphs/m<sup>2</sup> in fishless lakes and 0.98 nymphs/m<sup>2</sup> in fish-containing lakes (Appendix E). Mayflies were found in only two of the fish-containing lakes, whereas all fishless lakes had mayflies. Ninety-eight percent of the mayflies were *Callibaetis ferrugineus*, and the rest were *A. edmundsii*. *C. ferrugineus* occurred in 11 of 12 fishless lakes, and *A. edmundsii* occurred in 4 of 12 fishless lakes. Our estimates of the current and historic levels of mayfly production indicate that as a direct result of the introduction of trout, landscape-level mayfly productivity from the littoral zone of alpine lakes has decreased ~70% from historic levels (44% lower bound decrease, 84% upper bound decrease; Appendix E).

Other than mayflies, the only macroinvertebrate that differed in density between lake types were water boatmen (Hemiptera: Corixidae), with 1.22 individuals/m<sup>2</sup> in fishless lakes and 0.04 individuals/m<sup>2</sup> in fish-containing lakes (Wilcoxon-Mann-Whitney two-sample test  $Z = -3.2642$ ,  $P = 0.0011$ ; Appendix E). Other dominant macroinvertebrates included midges (Diptera: Chironomidae), alderflies (Megaloptera: Sialidae: *Sialis*), caddisflies (Trichoptera: Limnephilidae and Polycentropidae), dytiscid beetles (Coleoptera: Dytiscidae), and damselflies (Odonata: Coenagrionidae: *Enallagma*). These results are discussed in Appendix E.

#### Distribution of Rosy-Finches

Our prediction that Rosy-Finches preferentially forage at lakes with more mayflies was supported by the multiple regression analysis. The number of foraging Rosy-Finches at a lake varied across lake pairs, but increased significantly with the number of mayfly nymphs collected (Appendix F). The best-fitting model did not include covariates (Appendix F). Furthermore, covariates were not significantly related to Rosy-Finch abundance in any of the models that tested this relationship.

Overall, there were fewer Rosy-Finches at fish-containing lakes than at fishless lakes (Table 1). The effect of lake type on the number of Rosy-Finches varied with the period of mayfly emergence (Table 1). The magnitude of this interaction also varied across years (Table 1, Fig. 2). In all three years there were significantly more Rosy-Finches at fishless lakes than at fish-containing lakes during mayfly emergence but not before or after mayfly emergence (Table 2, Fig. 2). Across the three years of this study, 5.9 times more Rosy-Finches were observed at fishless lakes than at fish-containing lakes during the mayfly emergence period (Fig. 2). Although the best-fitting mixed-effects model included two covariates (tree density and the ratio of lake perimeter to surface area; Appendix F), these physical habitat characteristics were not significantly related to Rosy-Finch distribution (Table 1).

TABLE 1. Results of the best-fitting general linear mixed-effects model used to analyze repeated-measures data from all years of the study.

Effect	df		F	P
	Numer-ator	Denom-inator		
Time period	2	27.2	26.35	<0.0001
Lake type	1	19.8	30.66	<0.0001
Year	2	31.7	11.51	0.0002
Time period × lake type	2	20.5	30.8	<0.0001
Lake type × year	2	33.8	11.9	0.0001
Time period × year	3	38	10.28	<0.0001
Lake type × time period × year	3	40.6	15.91	<0.0001
Tree density	1	17.3	4.03	0.0604
Lake perimeter:surface area	1	22.7	0.36	0.5526

Note: Gray-crowned Rosy-Finch abundance (mean per 10-min count) predicted as a function of time period (before, during, and after mayfly emergence), lake type (fish-containing or fishless), year, their interactions, and two habitat parameters.

#### DISCUSSION

Organisms may be dependent on seasonally occurring, cross-boundary resources, especially if the resource shows a pulse during a critical life history stage of the consumer. If the subsidy exceeds the rate of local productivity of comparable resources, then the effects of the subsidy may be magnified across the productivity gradient between the donor and recipient habitats, triggering a consumer response in the recipient habitat (Ballinger and Lake 2006, Marczak et al. 2007, Yang et al. 2008). While terrestrial resources commonly subsidize aquatic ecosystems (e.g., Minshall 1967, Vannote et al. 1980, Carpenter et al. 2005), resource inputs from aquatic systems may also have an important influence on terrestrial consumers and the structure and function of terrestrial ecosystems (e.g., McCarty 1997, Polis et al. 1997, Willson et al. 1998, Henschel et al. 2001, Nakano and Murakami 2001, Sabo and Power 2002, Christie et al. 2008).

Our study clearly demonstrated the importance of a one-way flux of resources from a lentic donor system to consumers in a terrestrial recipient system. Consistent with Knapp et al. (2001b), Caudill (2003, 2005), and Finlay and Vredenburg (2007), we showed that mayflies occur primarily in fishless lakes. Coexistence of mayflies and trout at two of the fish-containing lakes is likely associated with the low density of trout in those lakes (see Caudill 2005). Our calculations suggest that in the study region, mayfly production has been reduced by 70% as a result of trout introductions. As an indirect consequence of their effect on mayfly production, introduced trout caused an 83% average decrease in the number of foraging Rosy-Finches at lakes with fish relative to those without fish. These findings support our prediction that Rosy-Finch foraging activity at a lake is directly and positively related to the emergence of adult

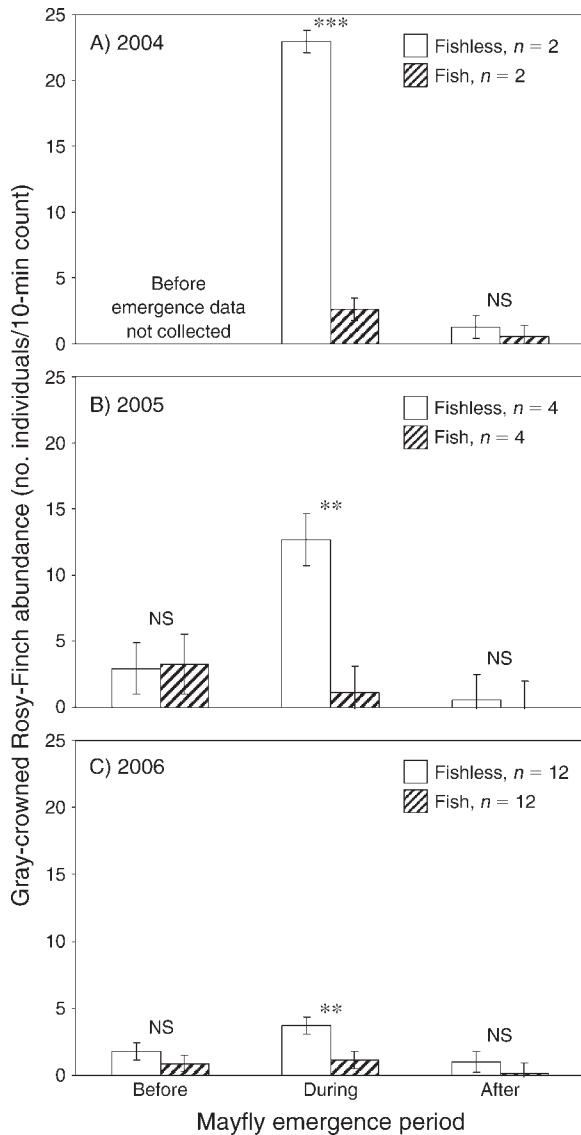


FIG. 2. Mean number of Gray-crowned Rosy-Finches observed at fishless vs. fish-containing lakes before, during, and after the period of mayfly emergence in (A) 2004, (B) 2005, and (C) 2006. Bars indicate means  $\pm$  standard error. Significance determinations and standard errors were based on least-square means pairwise comparisons between lake types at each stage of mayfly emergence, calculated from separate general linear mixed effects models for each year. Significance was evaluated with a Bonferroni correction.

\*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; NS, not significant at  $P > 0.05$ .

mayflies, and indirectly and negatively related to fish presence.

Rosy-Finch distributions are clearly altered by the presence of fish, raising the possibility that there are also population-level consequences of fish introductions for Rosy-Finches. In birds, greater food availability may increase the density of reproducing consumers (Fretwell and Lucas 1970, Knight 1988) or the reproductive output per consumer (i.e., a numerical response; Wiehn

and Korpimäki 1997). Furthermore, consumers can respond both functionally and numerically to predictable resource subsidies (Huxel and McCann 1998, Sabo and Power 2002). Conversely, we suggest that the widespread decrease in mayflies caused by intensive fish stocking may have caused either a negative numerical response in Rosy-Finches or a decreased density of nesting Rosy-Finches. It is common for adult passerines to feed insects to their young because insects, relative to seeds, are a high-quality, protein-rich resource with high assimilation efficiency, especially for chicks (Diaz 1996). In each year of our study, the mayfly emergence coincided with either the provisioning of nestlings or with the fledging period when chicks are still provisioned by adults (P. Epanchin, *personal observation*). Rosy-Finches may well depend on the mayfly subsidy to feed and successfully raise their young during the short, single-brood breeding season and to improve their own body condition.

Rosy-Finches are well adapted to exploit the locally abundant, spatially and temporally patchy mayfly emergence events. The long-distance, opportunistic foraging behavior of Rosy-Finches, coupled with their sublingual food-carrying pouch, allows efficient mayfly consumption and delivery to their young (Miller 1941, Orians and Pearson 1979). Nesting Rosy-Finches have been observed to forage long distances (up to 5.5 km) from their nest site (Miller 1988). This suggests that Rosy-Finches seek out high-quality foraging patches and that travel costs are partially offset by the reward rate and food quality within these patches of emerging insects. With the widespread introduction of trout to the historically fishless lakes of the Sierra Nevada and its concomitant effects on mayfly distribution and biomass, Rosy-Finches have undoubtedly experienced reduced access to concentrated sources of mayfly prey. The necessity of flying to the fewer, more widely dispersed, fishless, mayfly-rich habitats has almost certainly increased travel costs and could result in less frequent or reduced mayfly feedings to young, possibly to the point at which increased travel time and foraging costs are no longer offset by the net energy gained in a foraging patch (Orians and Pearson 1979).

The results of our study show that fish introductions have dramatically altered the nature of the boundary

TABLE 2. Least-square means pairwise comparisons of Gray-crowned Rosy-Finch abundance (mean per 10-min count) between lake types (fish vs. fishless) during the same stage of mayfly emergence (before, during, after).

Years	Mayfly emergence time period	Denominator df	<i>t</i>	<i>P</i>
2005–2006	before	42.3	−0.16	0.8732
2004–2006	during	27.7	−8.15	<0.0001
2004–2006	after	24.1	−0.6	0.5524

Note: Significance was evaluated using a Bonferroni correction ( $P < 0.017$ ).

between aquatic and terrestrial ecosystems. At fishless lakes, the boundary between aquatic and adjacent terrestrial ecosystems is poorly defined due to the export of lake-derived resources into the adjacent terrestrial landscape where they are exploited by the highly mobile Rosy-Finch as well as other birds and small mammals (P. Epanchin, *personal observation*). In contrast, this boundary is very pronounced at fish-containing lakes where fewer resources are available for transfer, and lake-to-terrestrial trophic transfers are few to nonexistent (as also suggested by Finlay and Vredenburg 2007). Therefore, the introduction of a nonnative top predator into donor systems may confine species interactions to that system, if the consumed prey otherwise would have been exported. The confinement of species interactions may be a general consequence of top predator introductions to systems occupied by organisms that do not have an appropriate behavioral response to avoid predation (e.g., McPeck 1990, Sih et al. 2000, Caudill and Peckarsky 2003). In the absence of such predators, however, adjacent food webs may be significantly connected, both directly and indirectly (e.g., Polis et al. 1997). The length and pathways of trophic interactions within and between donor and recipient habitats likely go beyond the simple tri-trophic system that we studied here (for example the detrital food web must be involved).

In conclusion, the effects of nonnative species introduced to a donor system can permeate into resource-limited recipient ecosystems in unexpected ways. In our study, the Rosy-Finch, a generalist cardueline finch species, typically thought of as a seed eater, was indirectly affected by fish introductions. Given that nonnative fish have been introduced globally to naturally fishless water bodies, we expect similar responses in other mountain ecosystems around the world. These results indicate the pressing need to consider cross-boundary subsidies when making decisions regarding fish stocking or lake restoration via fish removal. In the Sierra Nevada and elsewhere, fish-removal efforts have been implemented with the specific goal of recovering native amphibian populations (Vredenburg 2004, Welsh et al. 2006, Knapp et al. 2007). While important, we suggest that the goal of fish removal efforts, both here and in similar systems, be expanded to include the restoration of linkages between aquatic and terrestrial food webs.

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#### APPENDIX A

Map and physical characteristics of study lakes (*Ecological Archives* E091-172-A1).

#### APPENDIX B

Photo of a floating aquatic-insect emergence trap (*Ecological Archives* E091-172-A2).

#### APPENDIX C

AIC<sub>c</sub> rankings of models testing the relationship between fish presence and habitat variables (*Ecological Archives* E091-172-A3).

#### APPENDIX D

Analyses of the relationship between mayfly nymph density and fish presence (*Ecological Archives* E091-172-A4).

#### APPENDIX E

Effects of fish on mayflies and other benthic macroinvertebrates (*Ecological Archives* E091-172-A5).

#### APPENDIX F

Analyses of the effect of mayfly density and their emergence on Gray-crowned Rosy-Finch abundance (*Ecological Archives* E091-172-A6).