Grass type, vegetation cover, and predation affect abundance of *Microtus californicus* and *Thomomys bottae* in a coastal Mediterranean ecosystem

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**Abstract**

Invasive grasses negatively impact ecosystems and have become dominant over native grasses in central California. This study measured vegetation cover, the extent of ungulate grazing, vegetation height, and predation in invasive and native grasses and examined the response of Pocket gophers (*Thomomys bottae*) and California meadow voles (*Microtus californicus*) to invasive and native grasses. It was predicted that both *T. bottae* and *M. californicus* are more abundant in native grasses compared with invasive grasses. This study also predicted that *M. californicus* would prefer less grazed grasses, but *T. bottae* would prefer grazed grass. Finally, it was predicted that there would be a negative relationship between predatory bird activity and small mammal abundance. Results suggested that both *T. bottae* and *M. californicus* preferred mixed grasses, *M. californicus* preferred Harding grass (*Phlalaris aquatica*), which is an invasive grass type. Furthermore, vegetation cover, but not tallest grass height, affected small mammal abundance. Results indicated a negative relationship between the presence of *T. bottae* and *M. californicus*. However, there was a positive relationship between predatory bird activity and small mammal abundance. It was proposed that other factors such as location of the native grass affected small mammal abundance. The negative relationship between *T. bottae* and *M. californicus* was thought to result from *T. bottae* reduction of vegetation cover, which caused a

**Discoveries**

Although it has been shown that invasive plant species change established patterns of species composition, there is limited data that explores the physical factors of invasive species that influence population fluctuations. This paper examines the abundance of small mammals in native and invasive grass species. It further examines how vegetation cover, grass height, the presence of predation and of other small mammals in both native and invasive grass species affect small mammal abundance. The findings suggest that many factors including whether the grass is native or invasive, vegetation density, predation, and presence of other small mammals affect small mammal abundance. Invasive species management should consider physical differences between habitats with native compared with invasive grasses when implementing invasive species management techniques.
reduction in food supply and shelter from predatory birds. Studying the negative impact of invasive grasses on ecological systems in central California is a critical step towards developing invasive species management techniques.

For decades, ecological research has examined the abundance of small mammal populations. Research has shown that vegetation type (1), competition within and between species (2,3) and predation (4) are important factors in predicting abundance of small mammals. Small mammals have remarkable effects on their environment. Pocket gophers (Thomomys bottae) negatively impact plant communities and soil quality, a source of nutrients for many small organisms (2). California meadow voles (Mictomys californicus) are considered agricultural pests which can cause harm when their populations peak (5). Although these species are thought of as pests, they are keystone prey species that are important to California ecosystems (6). All species within an ecosystem rely on each other; however, a keystone species has a disproportionately large impact on its habitat (35). Keystone species T. bottae and M. californicus affect vegetation growth, are a food source for many predators and are hosts to many parasites (7).

Currently, in central California, native grassland vegetation has mostly been replaced with non-native annual grasses (5,8). Specifically, on the Rancho Marino Reserve in Cambria, California, Harding (Phlaris aquatica), Kikuyu (Pennisetum clandestinum) and Italian Rye (Lolium multiflorum) grasses are replacing native California grasses. Within central California, invasive grass species have been shown to change established patterns of species composition (9). As a result, extremely low and variable capture rates of small mammals have been found, indicating that invasive grasses likely provide poor conditions for small mammals (5), including sources of food and shelter (10). In historically settled grasslands, large mammal grazing also affects small mammal abundance and this varies by vegetation type (11). It is known that M. californicus are negatively affected by grazing (11,12,13). However, few studies have examined the effect of grazing on T. bottae, and results of these studies have been inconclusive. While one study showed a negative relationship between grazing and T. bottae (14), another study showed that T. bottae abundance was higher in grazed than less grazed meadows (11). Predation by predatory birds can also profoundly affect small mammal populations (4), and the presence of predatory birds can lead to a marked decline in small mammal abundances (15).

Here we predict that vegetation plays a role in small mammal abundance. Specifically, that T. bottae and M. californicus are both more abundant in native and mixed grasses than invasive grass species. We further predict a negative association between predatory birds and small mammals.

Method

Site Description

Data were collected at the Rancho Marino Reserve (RMR) in Cambria, California, which is managed by the University of California, Santa Barbara. The RMR is 500 acres, including 1.5 km of coastline, and is made up of Monterey pine forest and coastal terrace prairie. Sampling occurred over three days during August 2012. Six vegetation types were examined including grazed and less grazed P. aquatica, P. clandestinum, and L. multiflorum—all of which are invasive grasses. A location made up of predominantly native grass and a location made up of a mixture of native and invasive grass types was also included. Phalaris aquatic, originally from North Africa, is a tall (90–120 cm) perennial clump grass (16). Pennisetum clandestinum is an aggressive perennial plant with a dense, complex root system that forms a thick mat (17). Lolium multiflorum is a tall annual grass native to temperate Europe that behaves like a short-lived perennial grass (18). All locations sampled were situated within 2 km of the NW boarder of the RMR and less than 500 m from the shoreline (Figure 1).

Data Collection

The study measured M. californicus and T. bottae abundance in each vegetation type. Data were collected using a blocked quadrat sampling technique and measured along ten 20 x 2 metre transects at each vegetation type. Transects were five metres apart and two metres from the edge of each location to avoid pseudo-replication and edge effects. The density of M. californicus trails and holes as well as T. bottae mound abundance and size were assumed to be representative of the relative population abundances of each species. A M. californicus trail was operationally defined as a distinct, narrow, and well-worn pathway with clipped vegetation. A M. californicus hole was defined as a fresh hole in the ground with a diameter of 7 cm or less. A T. bottae mound was defined as a large accumulation of soil with less than 25% vegetation coverage. One vertical peak—the pointed top of a pile—was counted as one mound regardless of
whether the mounds were touching. Trails, holes and mounds that fell within or crossed over the transect boundary were included. Within each quadrat, percent vegetation cover was estimated to the nearest 5%. Vegetation height was determined by measuring the tallest grass in each quadrat. Predatory bird counts were measured three times a day (dawn, noon and dusk) for a period of 30 minutes for three consecutive days to determine predatory bird activity over each vegetation type. A predatory bird was counted as any bird with a flat silhouette and whose activity was scored each time their flight path intercepted a 20 m vertical plot boundary within each 30-minute sampling period. A discrete activity was counted when a predatory bird crossed the plot boundary more than once or if it stayed over the vegetation type for longer than 30 seconds.

Statistical Analysis

Two whole model tests were performed using a Generalized Linear Mixed Model (GLMM). The first whole model test examined the effect of location, vegetation cover, and tallest grass height on the abundance of *M. californicus* and *T. bottae*. The second examined the effect of location, vegetation cover, and tallest grass height on size of *T. bottae* mounds. A logistic regression was used to measure the effect of *T. bottae* mound size on the presence of *M. californicus* at each location. A linear regression was performed to examine the relationship between predatory bird activity and small mammal abundance. Data were analyzed using JMP statistical program (19). An alpha of 0.05 was set as the threshold of significance.

Results

The GLMM whole model test that measured the effect of location, vegetation cover, and grass height on small mammal presence was significant (GLMM, likelihood-ratio $X^2=290.924$, df=13, $p<0.0001$). Location and vegetation cover had a significant effect on small mammal abundance (likelihood-ratio $X^2=22.233$, df=5, $p<0.001$; likelihood-ratio $X^2=109.187$, df=1, $p<0.0001$). There was a significant interaction of location and small mammal type (*T. bottae* or *M. californicus*) on relative small mammal abundance (likelihood-ratio $X^2=11.594$, df=5, $p<0.05$). Small mammal abundance and tallest grass height were not significant (likelihood-ratio $X^2=0.012$, df=1, $p>0.913$; likelihood-ratio $X^2=0.105$, df=1, $p<0.746$). The second GLMM whole model test examined effect of location, vegetation cover and tallest grass height on *T. bottae* mound size and was also significant (GLMM, likelihood-ratio $X^2=106.829$, df=7, $p<0.0001$). Location and average density were significant predictors of gopher mound size, but grass height was not (likelihood-ratio $X^2=32.798$, df=5, $p<0.0001$; likelihood-ratio $X^2=38.624$, df=1, $p<0.0001$; likelihood-ratio $X^2=0.235$, $p<0.628$). Results of the GLMM indicated that small mammals tend to reside in certain locations over others, and *T. bottae* and *M. californicus* show a different pattern of habitat dispersion (Figure 2, 3). Furthermore, this model shows a correlation between vegetative cover and small mammal abundance (Figure 3). A logistic regression showed a significant negative effect of *T. bottae* mound size on *M. californicus* abundance at each location (likelihood-ratio $X^2=133.687$, df=11, $p<0.0001$). *Thomomys bottae* abundance significantly affected *M. californicus* abundance (likelihood-ratio $X^2=18.345$, df=1, $p<0.0001$). Furthermore, there was a significant interaction between location and *T. bottae* surface cover on *M. californicus* abundance (likelihood-ratio $X^2=56.676$, df=5, $p<0.0001$). There was a negative relationship between *T. bottae* and *M. californicus* at grazed *P. aquatica*, mixed grasses, *L. multiflorum* grass, but not at less grazed *P. aquatica*, *P. clandestinum* or native grasses (Figure 2).

A linear regression analysis revealed a significant positive relationship between predatory bird activity and small mammal abundance, $R^2=.15$, $F(1, 53) = 8.790$, $p<0.005$ (Figure 4). This implied that 15% of the variation in small mammal abundance was accounted...
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Figure 2. The frequency of Pocket gophers (Thomomys bottae) and California meadow voles (Microtus californicus) as a function of 6 vegetation types: Harding grazed (HG), Harding less grazed (HL), Kikuyu (K), Italian Rye (IR), native (N) and a mixed grass (M). Small mammal frequency was assessed from the abundance of M. californicus trails and holes and, T. bottae mounds. Thomomys bottae was most abundant in mixed grass while M. californicus was most abundant in less grazed Harding grass. There was a negative relationship between T. bottae and M. californicus (N=3000).

Figure 3. Frequency of Pocket gophers (Thomomys bottae) and California meadow vole (Microtus californicus) as a function of vegetation cover (%). The percent- age of vegetation cover was estimated from above (birdseye view). Microtus californicus abundance increased as vegetation cover increased while T. bottae abundance was greatest when vegetation cover was between 20-80% (N = 2863).

Figure 4. A positive relationship between small mammal abundance and predatory bird activity measured using a linear regression ($R^2=0.15$, $F(1,53) = 8.790$, $p<0.005$). Predatory bird activity was measured as a bird with a flat silhouette crossing a 20x20m vertical plot boundary within a 30-minute sampling period collected over 3 days at dawn, mid-day and dusk.

Discussion

Thomomys bottae abundance was greatest in mixed grasses, followed by grazed P. aquatica grass, while M. californicus abundance was greatest in less grazed P. aquatica. This is consistent with the findings that M. californicus tend to live in ungrazed grasses and T. bottae tend to live in grazed grasses (11,12,13). However, these findings contradict the prediction that both species would prefer native grasses. A potential explanation for this finding is that, although the native grass location was predominantly native bunch grass, other invasive grasses were present. Furthermore, studies have shown that some invasive species, including L. multiflorum, are the preferred diet of M. californicus (20).

An alternative explanation for why this finding was inconsistent with the body of literature on this topic is that the native bunch grass was located close to the shoreline, within 10 meters from the top of a high ridge. It is possible that M. californicus and T. bottae were not abundant in native grasses because of this habitat difference that is unrelated to grass type. A final explanation for the small abundance of small
mammals in native grass is that predatory birds tend to fly along the shoreline because they eat fish and amphibians in addition to small mammals (21). Therefore, perhaps small mammals were not abundant in native grass because of the increased threat of predation.

There was a negative relationship between T. bottae and M. californicus in areas where rodent density was highest, but this negative relationship did not occur in locations where rodent presence was sparse. The negative relationship was consistent with a longitudinal study that indicated that, on a broad temporal scale, a larger number of T. bottae mounds predicted a smaller M. californicus population in the following year (2). This study hypothesized that gopher mounds changed the vegetation structure of the area and made the habitat less desirable for M. californicus. The current study showed that vegetation cover affected small mammal abundance but that tallest grass height did not. Microtus californicus was not observed when vegetative cover was less than 61%. This pattern has been observed in numerous previous studies (22,23,24,25). A suggested reason behind this preference is that M. californicus use the dense vegetation as cover against predators. When gophers make mounds, they remove vegetation, which likely makes a habitat less desirable for M. californicus because it decreases food availability and shelter from predation. A different study used a mark-recapture technique over a small temporal duration and found a significant positive association between new gopher mounds and male M. californicus activity (26). This indicates that perhaps M. californicus are initially interested in new burrows, but over time, the T. bottae reduce vegetation, and disturb the soil (27) causing the habitat to degrade and the abundance of M. californicus to decline.

In contrast to our hypothesis, we found a positive relationship between small mammal abundance and predatory bird activity. When examining the relationship between small mammal abundance and predation, it is important to consider the fluctuating nature of small mammal populations. The literature is consistent in stating that predation does not impact the population when the small mammal population increases but is likely involved in the mechanism behind small mammal population decreases (28,29). It is therefore difficult to predict the relationship between small mammals and predatory birds at any given time without first knowing the state of the small mammal population cycle. However, predatory birds have been found to follow the most abundant food source (30,31,32). It is clear that vegetation cover has been suggested to be an important factor contributing to the vulnerability of small mammals to predatory birds (15). In the present study, as percent vegetation cover...
decreases, small mammal abundance and predatory bird activity increases (Figure 5). It is probable that burrowing decreases vegetation cover, which increases activity of predatory birds. Less grazed *P. aquatica* is an outlier in this ecological model, likely because it has a high density of *M. californicus* but a low density of *T. bottae* resulting in intact vegetation (Figure 2).

The current study tested the predictions that vegetation plays a role in small mammal abundance, specifically, that *T. bottae* and *M. californicus* are both more abundant in native and mixed grasses than invasive grass species and that there would be a positive association between predatory birds and small mammals. It was found that *T. bottae* and *M. californicus* showed differential preferences for various grass types and that in rodent abundant locations there was a negative relationship between *T. bottae* and *M. californicus*. Furthermore, this study showed a negative relationship between small mammal abundance and vegetation cover and a positive relationship between small mammal abundance and predatory bird activity.

Conclusions

Invasive grass species have almost completely taken over the grassland vegetation in California (5) and have been shown to reduce biomass in addition to decreasing the soil quality (33). Furthermore, control of invasive grasses poses a significant financial burden to land managers (34). To responsibly undertake invasive species management programs, it is crucial to first understand how invaders affect native species. Here, we examined small mammal abundance in native and invasive grasses and found that both positive and negative interactions. Given the limitations of the study, such as the limited number of study sites, the short duration of data collection, and the focus on aboveground factors, additional research should be conducted to further explore the impact of these and other variables on the distribution and abundance of *M. californicus* and *T. bottae* in central coastal California, and the role of invasive grasses play in their population cycles. Although small mammals are pests, they are also key-stone species. To maintain the ecosystem on the Rancho Marino Reserve in Northern California, it is critical to study factors such as grass type and predation that affect small mammal abundance. At this time, it is unclear whether restoration of native grasses would increase small mammal populations. Future research should experimentally measure whether small mammal population cycles are altered by the restoration of native grass species.

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Literature Cited


