

TITLE: Contrasting ecological roles of non-native ungulates in a novel ecosystem

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Summary

Conservation has long focused on preserving or restoring pristine ecosystems. However, understanding and managing novel ecosystems has grown in importance as they outnumber pristine ecosystems worldwide. While non-native species may be neutral or detrimental in pristine ecosystems, it is possible that even notorious invaders could play beneficial or mixed roles in novel ecosystems. We examined the effects of two long-established non-native species – Philippine deer (*Rusa marianna*) and feral pigs (*Sus scrofa*) – in Guam, Micronesia, where native vertebrate frugivores are functionally absent leaving forests devoid of seed dispersers. We compared the roles of deer and pigs on seedling survival, seed dispersal, and plant community structure in limestone karst forests. Deer, even at low abundances, had pronounced negative impacts on forest communities by decreasing seedling and vine abundance. In contrast, pigs showed no such relationship. Also, many viable seeds were found in pig scats whereas few were found in deer scats, suggesting that pigs, but not deer, provide an ecosystem function – seed dispersal – that has been lost from Guam. Our study presents a discrepancy between the roles of two non-native species that are traditionally managed as a single entity, suggesting that ecological function, rather than identity as a non-native, may be more important to consider in managing novel systems.

Introduction

The extent of human influence is so pervasive that the earth today is comprised mostly of novel ecosystems [1] – anthropogenically modified systems with species compositions and relative abundances that have not been previously observed [2]. Species introductions create and maintain novel ecosystems both by adding new species and by removing native ones [1]. Novel ecosystems typically still harbour many native species [3]; however, effective management of these systems is challenging due to the potentially new ecological roles of the remnant native and introduced species that comprise them.

Although the negative impacts of introduced species are extensive, some may also play beneficial roles [4]. Introduced species can be preferred candidates for restoring severely degraded habitats [5]. For example, non-native trees have been used in abandoned pastures where the native plants would not have originally facilitated the return of native plant communities [6]. Some introduced species may provide desirable ecological functions such as seed dispersal or food sources for native species [7]. The introduced Japanese white-eyes (*Zosterops japonica*) in Hawaii are seed dispersers for native plants that previously relied on now extinct or rare native birds [8]. Finally, invasive species may slow or reverse negative ecological effects from other anthropogenic impacts. Cascading ecological effects from overfishing in Cape Cod salt marshes are being reversed by green crabs (*Carcinus maenas*), which are normally considered a harmful invasive [9].

The negative effects of introduced deer and pigs have been well documented in ecosystems across the globe [10-13]. Deer alter forest structure by browsing on seedlings and saplings, and suppressing forest regeneration [14]. Introduced deer in New Zealand had effects on understory and forest composition that persisted even after control of deer (*Cervus elaphus*)

populations [15]. Similarly, pigs are known to affect regeneration and recruitment in a number of forest systems. For example, feral pigs have a pronounced effect on regeneration in lowland forests of Malaysia, by direct predation on seeds and by soil-rooting [16,17]. Rooting kills or physically damages seedlings and alters soil properties [18,19].

The southernmost island of the Mariana Archipelago, Guam, as with many islands around the world, has had a long history of species introductions [23], making its forests prime examples of novel ecosystems, albeit with unique challenges. One of the world's most infamous invasive species is the brown treesnake (*Boiga irregularis*), which was unintentionally introduced to Guam on military cargo at the end of World War II [24]. It is responsible for the extinction of most of Guam's native birds between 1945 and 1985 [25,26], functionally leaving the island bereft of native vertebrate nectarivores, frugivores, or insectivores [23]. While snakes are a relatively recent introduction, Philippine deer (*Rusa marianna*) (referred to as deer from here on) and feral pigs (*Sus scrofa*) (referred to as pigs from here on) have been established for centuries in Guam [20,22,27]. Deer were introduced to the wild in Guam in 1772 by Spanish Governor Mariano Tobias as game [22], while pigs in the forests of Guam are descended from livestock brought by Spanish colonizers in the 1660's, and subsequently mixed with other livestock throughout the centuries [20]. We have no evidence that wild boar have ever been introduced to Guam.

Like ungulates in other systems, both deer and pigs are thought to have negative effects on plant communities in Guam [20-22]. Deer density in Guam has been correlated with reduced seedling recruitment in some species of native trees [21,28]. Pigs in Guam, similar to pigs in other systems, alter habitats by rooting and wallowing [20], which can disrupt forest regeneration. However, the effects from deer and pigs are occurring within novel rather than

pristine ecosystems, therefore a more thorough examination of the role of each species within the larger ecological context is needed to make appropriate management decisions.

We investigated the ecological role of non-native ungulates in the novel ecosystems of Guam by examining the influence of non-native deer and pigs on seedling survival, seed dispersal, and seedling abundance in limestone karst communities. First, we experimentally tested whether deer and pigs affect seedling survival of a specific subset of native and non-native plants. We also tested the capabilities of deer and pigs for dispersing seeds by germinating scats collected in the wild. Finally, we compared plant community characteristics (e.g. native and non-native seedling abundance, vine abundance) across a range of relative ungulate densities to assess whether the effects of ungulates as herbivores or dispersers is evident in the forest.

Methods

Study area

Guam (13.5° N, 144.8° E; 544 km²) is the largest and southernmost island of the Mariana Island Archipelago in the Western Pacific. The dominant forest type of Guam is limestone karst forest. Plant communities in these forests are growing on top of calcareous rock – the brittle, fossilized remains of ancient marine organisms. This karst is extremely porous and easily weathered by water, creating sharp features that hold very little topsoil [30,32]. It is extremely rugged, with small crevasses and holes throughout. While a variety of karst types exist in northern Guam, our seedling plot and transect sites all occurred on reef facies and detrital facies of what is classified as Mariana Limestone – that is, Plio-Pleistocene reef and lagoon that comprises 75% of Guam's karst formations [33].

Guam's karst forests were chosen as the focus of this study because they contain a larger variety of native and endemic tree species relative to other habitats, such as savannah or ravine

forest [29,31]. We chose sites for this project that were considered native limestone karst forest in order to maintain similarities between sites and maximize the likelihood of discerning differences due to pig and deer abundance rather than other site characteristics like history of disturbance or species composition. Native trees still dominate these sites. However, the relative abundances of vegetation differ from early descriptions of Guam forests, suggesting that forests have changed over time [30,31]. This, combined with the presence of non-native plants, insects, and mammals [23] and the absence of birds provides an ideal setting for investigating roles of non-native species in a novel ecosystem.

Effect of ungulates on seedling survival

To assess ungulate effects on seedling survival, we set up paired plots in eight selected karst forest sites in northern Guam. At each site, we erected a 1.8-m tall chicken-wire fence around one plot, and left the adjacent plot unfenced, allowing ungulate access. Each seedling plot covered an area of about 3.5 m x 5.5 m. The fenced and unfenced plots were placed so that individual pairs had similar canopy cover, rockiness, slope, and ground cover, as well as similar adult tree composition, density, heights, and diameters. While species composition of adult trees already present was almost impossible to match exactly, species composition often overlapped. Using linear mixed effect models to compare the fenced and unfenced treatments, we found no significant differences in numbers of adult trees ($p=0.22$), canopy cover ($p=0.9191$), average diameter at breast height ($p=0.57$), and average height of adult trees ($p=0.98$) between paired plots. We avoided gaps, depressions in the substrate, or any other features that might have caused a difference between the paired plots outside of our treatments.

We selected six species for this experiment encompassing a variety of common native and one introduced tree that occur in Guam's karst forests: *Carica papaya*, *Morinda citrifolia*,

Ochrosia oppositifolia (synonym *Neisosperma oppositifolia*), *Aglaia mariannensis*, *Premna serratifolia*, and *Psychotria mariana*. All are common components of Guam's limestone karst forests, although the non-native *C. papaya* tends to favor edges, and *P. mariana* is less common than the other species. For each species, we collected seeds from at least five trees and at least four different sites to minimize maternal effects and effects of local adaptation. The date of seed collection and subsequent out-planting was staggered by species due to differences in fruiting phenology. Seeds were planted under 60% shade cloth at a nursery in Guam and allowed to grow in these conditions until they had fully rooted and grown their first true leaves. At this point, the seedlings were transported to the exclosure sites for out-planting.

Seedlings of each species were out-planted in the control and treatment areas at each site on the same day. Seedlings were placed at least 0.3 m apart from each other, and at least 0.5 m away from the fences in fenced treatments. Seedlings were haphazardly placed within the seedling plot since they had to be planted around rocky karst structures and roots from neighbouring trees. Fourteen seedlings of each species were planted in each treatment at each site, except for *O. oppositifolia*, a tree with large fruits and seeds, which had only nine seedlings planted per treatment. The seedlings planted during drier months (*C. papaya*, *M. citrifolia*, and *O. oppositifolia*) were watered about every other day during the first few weeks following transplanting to ensure they successfully established. Guam's "dry season" occurs roughly from December to May annually. We monitored seedling mortality monthly, but final counts used in analysis were recorded in July 2011, or 15 months after the first species was transplanted and four months after the last.

Seedling survival was compared for each planted species between fenced and unfenced plots, using generalized linear mixed effects models (lme4 package) in R [34]. Fencing was

considered a fixed effect, whereas site was considered a random effect. After determining that the effect of the treatment (fenced or unfenced) was not dependent upon the the duration of time seedlings were growing (Table 1), we analysed seedling survival for each species separately. Factors were considered to have a significant effect on seedling survival if they reduced Akaike Information Criterion, corrected for smaller sample sizes (AICc), scores by more than 2 in the corresponding model [35].

Germination from scats

We collected scats from deer and pigs from limestone karst forest sites to determine if either species dispersed viable seeds via endozoochory. We collected throughout the year, through both rainy and dry seasons from four sites in northern Guam. Scats were layered on top of a 50% perlite and 50% peat moss soil mix in germination trays. The trays were kept outdoors at a nursery under shade cloth. Deer pellets were admixed at the surface, pig scats were broken up and mixed at the surface. Trays were watered regularly before and after seedlings emerged from scats. Seedlings were then identified and counted. Because the nursery was open air, species that were known to be wind-dispersed and that germinated across all seedling trays, including adjacent experiments at the nursery, were not counted. We then compared the abundance of species germinating in scats to their natural abundances in nature, using our vegetation transect data.

Effects of ungulates on community composition

We surveyed the community composition of karst forest sites by using 100-m by 1-m belt transects at 14 different sites across northern Guam, where limestone karst dominates the forest types. All plants within these transects were identified to species and categorized by growth form (ie. vines, trees, shrubs, or herbs) and as native or non-native. Plants were considered seedlings if

they appeared to be within their first year of growth – for woody species, they had no woody stem yet, or were less than 0.5-m tall.

Scats from pigs and deer were counted along the vegetation transects described above. To detect a range of scat abundances, we also surveyed a greater area at each site by including 2-m-wide belt transects encircling the vegetation transects (see Figure 1). These were walked and length estimated using GPS, with total area surveyed amounting to approximately 800 m². However, since transect lengths used to count scats differed slightly from site to site, scat abundances used in analysis were number of scats per 100 m². Actual ungulate densities in any habitat in Guam is unknown and has rarely ever been attempted because common methods such as spotlighting, visual counts on transects, and aerial counts are challenging in dense tropical forests. Although they do not give exact population abundance, counts of scats can be used as an index to compare abundance of ungulates among sites [35]. We used scat as an indicator of ungulate abundance because other sign, such as animal tracks, are rarely visible in karst forest terrain and the detectability of other sign such as trails and browsing sign varies widely even in similar habitats [21].

We used linear regressions to determine whether ungulate scat abundance covaried with forest characteristics measured on vegetation transects. Deer scat abundance and pig scat abundance were considered as separate independent factors, and forest characteristics as dependent factors. The forest characteristics that we investigated were total seedling abundance, native seedling abundance, non-native seedling abundance, and vine abundance. For each correlation, we report r^2 values.

Permissions and licenses

We applied for and received special use permits to conduct research on U.S. Fish and Wildlife Service (Department of Interior) Wildlife Refuge property in 2010. This was coordinated through Refuge Manager Joseph Schwagerl (Joseph_Schwagerl@fws.gov) and Refuge Biologist Cari Eggleston (cari_eggleston@fws.gov). For study sites on Government of Guam property, we received approval from Guam Department of Agriculture for use of the Anao Conservation Area, and approval from the Chamorro Land Trust for use of Chamorro Land Trust lands. In addition, surveys carried out on Department of Defense property were coordinated with permission from U.S. Air Force, 36th Wing Civil Engineering Squadron, Environmental Flight.

Results

Effects of ungulates on seedling survival

Since planting dates were staggered, we included length of time in plots in a full model for predicting survival: treatment, species, and length of time in plots as predictive variables, with interactions between treatment and species, and between treatment and length of time. The best fit model included species, length of time in plots, treatment, and interaction between species and treatment (Table __). Length of time and species are correlated because planting was staggered due to species. However, a model with treatment by species was better fit than a model with treatment by time. We were interested primarily in treatment effects, and since species and length of time are correlated, we analyzed treatment effects separately for each species.

For four species, *C. papaya*, *M. citrifolia*, *P. serratifolia*, and *P. mariana*, fencing treatment contributed to the best-fit model explaining proportion alive (Figure 2), with higher survival of seedlings when protected from ungulates. For *A. mariannensis* and *O. oppositifolia*, AICc values were <2 between models including and not including treatment, indicating that

these two species did not benefit from protection from ungulates. Almost all mortality observed in seedling plots was in the form of deer herbivory – evident by leaves and stems being cut from the seedlings – instead of disturbed by uprooting by pigs.

Germination from scats

Only four of the 20 deer scats collected produced seedlings (20%), and only 13 seedlings germinated, from four different species of non-native plants and two unknown species (Table 2, Figure 3). Eight *Passiflora suberosa* seedlings germinated from one pellet group. In addition, one *C. papaya*, one *Vitex parviflora*, and one *Mikania micrantha* seedling each emerged from separate pellet groups. The *M. micrantha* may have been ingested by the deer accidentally, as this species has wind-borne seeds lacking a fruit. The wind-dispersed species that were common to many trays in the nursery, and were found separate from the scat samples within the planting trays, were excluded from this count. The *M. micrantha* seedling, however, was only found in one tray, sprouting directly from one of the deer pellets, and so was included.

Many more seedlings emerged from the 31 pig scats that we collected from four different sites. Of these, 25 scats had seedlings (80.6%), with a total of 1658 seedlings germinating (Table 2). Eight species germinated from pig scats. They were the native trees *M. citrifolia* (in 20 out of 31 scats), and *Ficus prolixa* (in three scats); the non-native trees *C. papaya* (in 16 scats) and *Leucaena leucocephala* (in one scat); the non-native vines *Passiflora* spp. (in three scats) and *Coccinia grandis* (in three scats); and the non-native herb *Chromolaena odorata* (in one scat). All of these except for *C. odorata* and *L. leucocephala* have edible, fleshy fruits.

We used data from our vegetation surveys to compare the most abundant species that germinated from scats to the most abundant species found in nature (Figure 3). Proportional abundance in nature (left hand panel, Figure 3) for each species was calculated by dividing the

total count of adults of that species across our fourteen sites and dividing that by the total number of adult trees across all sites. (Total adult count of one species / total adult count of all species counted on vegetation transects). We counted only adult trees in calculations to represent potentially fruiting trees. We used a similar approach to calculate the proportional abundance of seedling species found in pig and deer scats: the total number of scats that has a given species of seedling germinating from it, divided by the total number of either deer or pig scats that we had collected. For example, *Carica papaya* seeds germinated in 16 out of 31 pigs scats. Therefore, the proportional abundance was 16 divided by 31, or 0.52. Because multiple species occurred in some single scats, the values for proportional abundance in scats do not necessarily add up to 1. The species found in the highest proportion of scats for both deer and pigs did not reflect the most abundant species in nature, suggesting some selection for certain species.

Effects of ungulates on community composition

Strong negative loglinear relationships were detected between the following forest community abundances and deer scat counts: total seedling abundance ($r^2 = 0.707$, $P < 0.001$), native seedling abundance ($r^2 = 0.649$, $P < 0.001$), non-native seedling abundance ($r^2 = 0.792$, $P < 0.001$), and vine abundance ($r^2 = 0.792$, $P < 0.001$) (Figure 4). In contrast, no correlations were detected between these metrics and pig scat counts.

The two species for which seedling survival was unaffected by the ungulate exclosure treatment in the experiment above, *O. oppositifolia* and *A. marianensis*, are also dominant in nature. After *Meiogyne cylindrocarpa*, they comprise the top three most common tree species for adults across all sites, accounting for over 30% of adult tree species surveyed for this study (Figure 3, top panel). In addition, together, they accounted for over 60% of seedlings recorded in our transects in Guam, and were present even in the areas with the high deer abundance.

Discussion

We found that two non-native species often managed as a single entity – ungulates – differ in their effects at a species level. Deer selectively browse four of the six species tested while avoiding the other two (Figure 2), and as a result, have potential to shape forest community diversity through herbivory. When assessing seed dispersal, we found that deer dispersed very few seeds, while pigs dispersed large numbers of predominantly native seeds. The negative effects of deer were evident across the forest, as there were far more seedlings in areas with few deer than in areas with moderate or high pellet counts from deer, whereas no such correlations were detected with pig abundance (Figure 4). This, in combination with the observation that most mortality in the exclosure study appeared to come from browsing rather than rooting, indicates that deer have a greater impact on seedling mortality than do pigs. While the benefits of pigs as seed dispersers were not evident in the seedling community, neither was a negative role for pigs; herbivory by deer is likely to mask any benefits provided via dispersal by pigs. In a novel ecosystem completely lacking native seed dispersers, the negative effects of non-native deer on seedling presence and abundance and the potential for non-native pigs to fill a missing ecological function provide support for a management approach based on functional roles rather than native/non-native status.

Both native and non-native species germinated from pig scats, while a smaller number and diversity of seedlings that only included non-native species germinated from deer scats. The most abundant seedlings in pig scats were from species that produce fruit containing numerous small seeds. The high number of small seeds in a given *M. citrifolia*, *Ficus* sp., or *C. papaya* fruit means that there are many opportunities for germination once a single fruit is encountered by a pig in the forest. *M. citrifolia* has an average of about 120, *Ficus prolixa* has about 190 and *C.*

papaya has about 700 seeds per fruit (unpub. data). Both *M. citrifolia* and *C. papaya* are known to grow easily in disturbed or edge areas [36,37]. Although *C. papaya* is not a native plant, it is naturalized and not considered invasive in the Marianas [31]. It is common in Guam in previously disturbed areas and edges but not in deeper forests [29,31], indicating that it may be important for primary or secondary succession and forest regrowth in disturbed areas. This, coupled with the results of our seedling plots indicating that both *C. papaya* and *M. citrifolia* are browsed by deer, suggests that while deer can inhibit regrowth in disturbed areas, pigs may be one of the few vertebrate species that could move successional species into edges and gaps.

Beyond ecology or status as native or non-native, traits of the plant species themselves turned out to be predictive of how they were affected by either deer or pigs. As mentioned above, *M. citrifolia*, *Ficus* sp., and *C. papaya* all contain a large number of small seeds per fruit, contributing to the numbers we recorded germinating from pig scats. They are also fleshy-fruited and sweet or pungent when ripe, suggesting appeal to pigs when encountered in the forest. Evidence also points to small seed size being advantageous to dispersal [38]. None of the seedling species that we planted had obvious physical defences such as thorns or spikes to deter herbivores. While species-specific studies have rarely been done on the chemical traits of species planted in our seedling plots, we assume that these characteristics contribute to their survival in the presence of deer. Studies on other species of deer suggest their selective browsing depends on chemical composition of different plants. For example, they tended to avoid plants with high amounts of tannic acid [39,40]. We do not have chemical composition studies on the two species that were consistently avoided in seedling exclosures (*O. oppositifolia* and *A. mariannensis*). However, *O. oppositifolia* has a thick, milky sap like other Apocynaceae, and other members of the *Aglaiia* genus are known to have high tannin content [42,43], potentially contributing to lower

palatability by deer. *M. citrifolia*, *P. serratifolia*, *C. papaya*, and other species of *Psychotria* have documented medicinal uses [27,44,45,46, 47], suggestive of potent chemical properties, but all were consumed by deer in our open seedling plots. This, rather than just origin or status as native, contributed to their susceptibility in Guam.

Because deer and pigs are being managed within the context of novel ecosystems, these functional differences suggest that different management strategies should apply to each species, especially in limestone karst forests. Deer are not replacing a lost ecological function, but instead have a strongly negative impact on forest communities by hindering forest regeneration (Figure 4). The two most common tree seedlings across all of our survey sites and two of the most common adult species in the forests on Guam (after *Meiogyne cylindrocarpa*) are the two species that survived just as well outside our seedling exclosures as they did inside – *O. oppositifolia* and *A. mariannensis*. This suggests that browsing preferences have already been shaping the forest species composition on Guam. Unfortunately, since both deer and pigs have been present for centuries, we had no true “ungulate-free” control. To remedy this, we used exclosures and gradients of abundance to tease apart what their effects are to plant communities. Our findings are consistent with many studies on the detrimental effects of invasive deer, primarily through selective browsing [10,11,14]. We anticipate that deer eradication or control to very low abundance would prove beneficial on Guam, which has never had native mammalian herbivores.

In contrast to deer, we did not detect strong negative impacts from pigs in the native limestone forest, and pigs are one of the last major vertebrate dispersers on an island that has lost its native dispersers. We know that pigs are present in these forests, and their wallows are abundant in ravine forests. However, unlike other forest types, the forest floor in a limestone karst forest is rocky and rigid [29,31], which would be difficult for pigs to root and wallow in,

thereby limiting the extent of their damage to seedlings. In contrast, feral pigs in Hawaii and Malaysia cause seedling mortality, increase erosion, affect biogeochemical cycling, and spread invasive plants [17,48-50]. These impacts are unlikely to be as severe in the rocky substrates of Guam's limestone karst forests. Rather, removing pigs from the limestone forests on Guam could have detrimental effects to plant species that have been limited by the lack of dispersers. We recognize pigs would likely have a greater impact in areas, such as secondary forest or volcanic forest, with more soil. However, the role of non-native species must be evaluated on the basis of each habitat and ecological situation, rather than on a species basis. We encourage more studies into the distribution, abundance, and potential seed dispersal capabilities of pigs in Guam.

Invasive species are normally managed with the goal of control or eradication, but in novel ecosystems with multiple species and factors contributing to ecological changes, a blanket approach may not be wise. Feral ungulates are components of novel ecosystems around the world, and although their negative effects are well-documented [51-53], there are a few examples where they play beneficial roles [54,55] or have unexpectedly insignificant effects on native flora [56,57]. While the novel ecosystems of Guam provide an important context in determining the relative detriment or benefit of these ungulates, the natural limestone karst forest features, which are easier for deer to traverse in, but more difficult for pigs to root and wallow in, also played a large role in determining this. A similar study in the clay soils of Guam would likely produce different results. Ungulate eradication is an important restoration tool, especially in island environments where ungulates are considered destructive invasive species [57]. Although this may still be the preferred management tool for Guam's systems, there may be unintended consequences. These include the release of invasive plant species [15,58] or reduced seed dispersal [53]. Natural resource managers would be aided by discerning which non-native

species serve important functions and which species are especially destructive in a particular habitat type, before implementing conservation actions in a novel ecosystem.

Most conservation goals emphasise reintroducing reduced or extirpated native species to historical abundances, and efforts that have focused on removing invasive species and reintroducing native species have yielded many positive results [57,59,60]. In the Marianas, management plans are focused on eradicating ungulates, and pigs are frequently the targeted ungulate species. However, removing invasive species could have negative consequences if these species play important ecological roles otherwise missing from the novel system [61]. In addition, while more research should be done on the importance of species traits in determining relationships between the plants in these ecosystems and their potential herbivores and dispersers, our results indicated that traits such as number of seeds per fruit, palatability, and morphology (vine/tree/herb) were, indeed, more important than native status in determining these relationships. If restoration of native species is a future possibility, non-native species may act as a temporary placeholder until species reintroductions can occur. Restoring a functioning ecosystem rather than the exact original complement of species, or considering restoration an iterative process with strategic and temporary use of non-natives, may be more feasible for highly degraded ecosystems [62].

Ethics

No animal or human subjects were used to carry out this study. This study was designed and written solely by the authors listed. See Methods section for permissions for use of government properties.

Competing Interests

We have no competing interests.

Data Availability

Complete datasets are available at <http://dx.doi.org/10.5061/dryad.sp5ff>.

Author's Contributions

Ann Marie Gawel helped to design the study, set up the experiments, collect data, analyse and draft the manuscript. Haldre Rogers helped design and coordinate the study, set up experiments, and aided in analysis and drafting the manuscript. Alexander Kerr aided in designing and coordinating the study, reviewing the analysis, and drafting and reviewing the manuscript. Ross Miller aided in designing and coordinating the study and reviewing the manuscript. All authors gave final approval for publication.

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