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Application of harmonic radar technology to monitor tree snail dispersal

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Abstract. Planned conservation efforts for tree snails of the endangered genus *Achatinella,* endemic to the island of O'ahu, Hawai'i, will include translocations among the remaining wild and captive-bred populations. In order to establish optimal levels of artificial migration among neighboring groups of snails within fragmented populations, efforts to determine natural dispersal rates through direct observation were initiated. Capture–mark–recapture (CMR) efforts have proved inadequate for obtaining the requisite dispersal estimates, due to low recapture probabilities. In addition, snail dispersal beyond the boundaries of a finite CMR study site was indistinguishable from mortality. In the preliminary study reported here, both the low recapture probability and dispersal detection problems of past CMR efforts were addressed by using harmonic radar tracking. This approach yielded rough dispersal estimates that were unattainable using CMR alone by providing 100% recapture rates even beyond the normal survey area boundaries. Extensive snail movements within clusters of connected trees were frequently observed after tracking for merely a few hours, although movements between unconnected trees were rare and recorded only after monthly survey intervals. Just 11 out of 40 tracked snails made between-tree movements (average distance of 4.94 ± 1.52 m) during the entire 7-month study, and provided the only data utilizable for inferring gene flow in and out of subpopulations. Meteorological data loggers were deployed when tracking began to look for an association between such snail movement and weather fluctuations. The resultant data indicate that increases in both wind gusts and humidity facilitate dispersal ($R^2 = 0.77$, p-value <0.001), and that passive wind dispersal alone may be responsible for many snail movements ($R^2 = 0.59$, p-value $= 0.0014$). Despite having provided coarse estimates of short-term dispersal and corresponding wind influences, the limitations of the radar method can be substantial.

Additional key words: telemetry, mark–recapture, wind dispersal, Achatinella

Tree snails of the genus *Achatinella* (Pulmonata: Achatinellidae), endemic to the island of O'ahu, Hawai'i, are rapidly disappearing and are all listed as Endangered by the United States Fish & Wildlife Service (USFWS 1992). Only ten species are extant out of the original 41 recognized by USFWS (based on synonymizations by Pilsbry & Cooke [1912–1914]). Initially common throughout native forests of both the Wai'anae and the Ko'olau mountains, *Achatinella* species can now be found only in scattered patches near the summits of these ranges. Following severe declines in number as a result of habitat loss and shell collecting in the 19th and 20th centuries, predation by introduced rats and the snail *Euglandina rosea* continue to decimate and fragment remnant snail populations (Hadfield 1986; USFWS 1992; Hadfield & Saufler 2008). The unusual life-history characteristics of these long-lived and late-maturing snails make any unaided recovery from invasive predator impacts extremely difficult (Hadfield et al. 1993). To assist in the preservation of the remaining wild populations, various governmental agencies have contributed to the initiation of both a captive-breeding program and building of predator-proof exclosures.

The intended goals of these conservation actions appear to have been achieved according to field and lab records (Hadfield et al. 2004), which show increases and/or stabilizations for some populations. However, the long-term consequences on the health

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of the gene pool from captivity, exclosures, and the fragmentation of subpopulations have yet to be addressed. There is growing concern that most of the remaining wild, enclosed, and captive populations of *Achatinella* spp. are increasingly at risk of the negative effects of inbreeding because of loss of genetic connectivity. Management strategies are being considered that will include translocation among neighboring subpopulations (residual fragments of historically continuous populations) to minimize the effects of excessive inbreeding, while being careful as to avoid any detrimental effects from unnatural levels of outbreeding. Storfer (1999) argued that only by first obtaining detailed observations of a species' natural gene flow can minimization of both these phenomena be accomplished. Microsatellite analyses using *Achatinella* spp. failed to reveal any structure on a subpopulation level (K.T. Hall, unpubl. data), rendering estimation of dispersal with modern genetic methods impossible. In light of this, a more direct approach was adopted to determine natural migration rates for two *Achatinella* spp.

Tree snails can be difficult to detect within dense vegetation, which makes obtaining direct dispersal-rate estimates difficult. Initial efforts using capture–mark–recapture (CMR) were hampered by low recapture rates, making any attempts at dispersal-rate estimation from those data imprecise (K.T. Hall, unpubl. data). Some snails were recaptured after not having been captured for several sampling intervals, most having returned to or never left their original trees, and others on neighboring or more distant trees. It is also often nearly impossible to distinguish between dispersal beyond a finite study site's boundaries and death (Koenig et al. 2000). This is especially true in animals such as small snails, whose remains are hard to locate. To increase the chances of recording more precise distances, frequencies, and timing of dispersal for *Achatinella* spp., harmonic radar tracking methods were adopted. The radar system includes a hand-held transmitter/receiver unit (Recco Inc., Lindingo, Sweden), which is used to detect small diode/wire combinations glued onto shells of live snails. With the expected 100% recapture rates, it was anticipated that preliminary estimates of short-term dispersal frequencies and distance could be obtained. Detection distances of up to 10 m were also readily possible with the radar, minimizing the reduced dispersal detection problems beyond the edges of a finite study site. However, the transponders receive and reflect a generic signal, and so individual identification must still rely on unique CMR codes.

Observations of dispersal during our pilot CMR surveys often varied following changes in observable weather conditions, implying that dispersal events may be a result of environmental factors. Prolonged periods of hot and dry conditions sometimes corresponded to an increased ratio of previously marked to unmarked adult snails in field surveys, as well as increased recapture rates (suggesting lower immigration). Similarly, stormy winter months sometimes led to an increase in the proportion of unmarked adults and reduced recapture rates (indicative of higher immigration). Therefore, it was hypothesized that any increases in snail movement detected with a harmonic radar would positively correlate with wind speed and humidity and/or negatively with temperature. Significant correlations would help determine whether dispersal is passive (i.e., positive correlation with wind gusts, which have been thought to blow snails out of trees [M.G. Hadfield, unpubl. data]) or active (i.e., positive correlation with high humidity, because some snails may be less active in the dry season [Cowie 1980]).

Methods

Transponder design

The results of successful studies using harmonic radar technology with a few land snail and insect taxa have already been published (e.g., Mascanzoni & Wallin 1986; Lovei et al. 1997; Stringer et al. 2004). O'Neal et al. (2004) conducted a study to optimize the trade-off between detection distance and transponder size to minimize any hindrance to the individual's natural movements, using a design very similar to the one adopted here for use with *Achatinella* spp. We tested many different kinds of transponders on captive individuals of *Achatinella* spp. before the current design was adopted. These transponders weigh <0.02 g, which is well below the conventionally accepted transmitter/body weight ratio (dubbed "the 5% rule") for having no adverse effects on the study organism. This rule, although informal, was adopted from studies on birds (Cochran 1980), small mammals (Aldridge & Brigham 1988), and fish (Claireaux & Lefrançois 1998). To determine snail weights, a series of living individuals of *Achatinella* spp. in the lab, all individuals ≥ 13 mm in shell length, were weighed and found to be >1 g. Therefore, only snails with shells ≥ 13 mm snails were fitted with transponders.

The transponders are passive and can theoretically function for several years without a power source. They are constructed from 6-cm lengths of a Teflon-coated, 0.08-mm-diameter copper wire (Omega Engineering Inc., Stamford, CT, USA) that were soldered

Fig. 1. Adult of *Achatinella mustelina* (21 mm in length from the apex to the bottom of the aperture) equipped with a harmonic radar transponder.

to small Schottky diodes (Mouser Electronics Inc., Mansfield, TX, USA) (e.g., Fig. 1). The solder bond is strengthened with a high-conductance epoxy resin, and the diode portion is glued with Satellite City Super T® to the body whorl of the snail's shell, oriented so that the wire drags behind the shell apex as the snail crawls. Transponders can be removed as needed by placing a drop of glue remover (Satellite City Super Solvent®) onto the glue bond, pushing away the resulting compound, and removing the transponder with slight pressure from tweezers.

Experimental approach

Achatinella mustelina Mighels 1845 (Wai'anae Mountains) and *Achatinella sowerbyana* Pfeiffer 1855 (Ko'olau Mountains) were used to monitor movement patterns. They are the only two remaining species of *Achatinella* with substantial numbers surviving in a fairly continuous habitat, providing the closest representation of gene flow in *Achatinella* before anthropogenic disturbances. The four field sites (Fig. 2) chosen include two replicates for each species, located at the extreme north/south ends of each species' known range to account for geographic and climatic variations. These are Palikea (in The Nature Conservancy's Honouliuli Preserve) and Kahanaha'iki (Makua Military Reservation) in the Wai'anae Mountains for *A. mustelina* (18 km apart), and north of the Poamoho monument (Ko'olau Summit Trail [KST]) and west of Opae'ula Cabin (Army leased land, leeward of the KST) in the Ko'olau Mountains for *A. sowerbyana* (2 km apart).

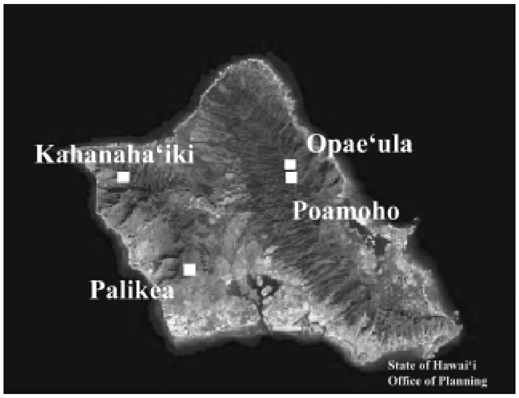

Fig. 2. O'ahu, Hawai'i. The four field sites used in this study are marked with squares.

For each site, perimeters were delineated by centering on the highest density area, with boundary extensions roughly corresponding to the maximum dispersal distances observed during CMR pilot studies. This is also the maximum amount of area that could be regularly searched with the manpower available. Within each site, a grid of $5\,\text{m} \times 5\,\text{m}$ quadrats was created. Individual quadrats were large enough to wholly contain most tree clusters. The actual number of quadrats at each site varied from 15 (Palikea) to 55 (Poamoho), due to each site's natural barriers (e.g., streams and cliffs). Ten of these quadrats were randomly selected (using a random number table to obtain individual quadrat numbers) at each of the four sites, and one snail $\geq$13 mm within each selected quadrat was fitted with a transponder (the maximum sample size allowed under USFWS permit TE826600). Daytime surveys were conducted at each site on a monthly basis to monitor dispersal (for $N = 40$ radar-equipped snails in total). In addition, two hourly overnight surveys were conducted at both Palikea and Kahanaha'iki to see whether any dispersal occurs during normal nocturnal foraging movements.

Weather/dispersal correlation

Weather data loggers from Onset Inc. (wind speed, humidity, and temperature, logging every 15 min) were deployed at three sites in early August 2006 to accumulate meteorological data (Poamoho snail tracking began in late August 2006). Radar-detected dispersal locations and weather data were recorded simultaneously at monthly intervals for a period of 7 months (through March 2007) to include both dry and wet seasons. The number of inter-tree dispersal events revealed with harmonic radar each month was recorded in addition to the corresponding weather values (minima, maxima, and averages) for that month to look for relationships (similar to Aubry et al. 2006). A best-subsets multiple regression procedure was used to select the model(s) that best explained the variation in monthly dispersal, based on Akaike's information criterion (Akaike 1974). This criterion provides a way to trade off the complexity of an estimated model against how well the model fits the data, preventing the appearance of a superior model that results from overfitting the data. All analyses were performed using R software (version 2.4.1, Ihaka & Gentleman 1996).

Results

Neither of the two hourly overnight surveys conducted at each Wai'anae site showed any movement of snails between unconnected trees, which would have required movement across the ground. Unconnected trees are defined as two clusters of vegetation that have no branches or leaves that come into contact with each other under normal weather conditions. Such between-tree movements were rare and only apparent after 1-month intervals. However, total linear movements as great as 3 m among connected trees were not uncommon in a single night. Based on the high frequency of movements throughout connected tree clusters, and the extreme rarity of finding live snails on the ground, inter-tree movement (between unconnected trees) became the focus of this study. As in other tree-snail studies exhibiting similar migration patterns (e.g., Schilthuizen et al. 2005), only these rare inter-tree movements have relevance to gene flow among subpopulations. Throughout this article, "dispersal" will refer only to movements between unconnected trees.

A list of all recorded snail dispersal and distances traveled by month is presented in Table 1. Inter-tree dispersal rates were between 0% and 20% per month, with more frequent dispersal occurring during the winter months when comparison was available (Wai'anae sites only). During this 7-month study, only 11 out of 40 snails were relocated outside of their original trees, providing a total of 17 between-tree movements. Dispersal distances were measured as the length between the two trees' bases at ground level, and resulted in an average of 4.94 ± 1.52 m.

For each month and site, the number of transponder-equipped snails (out of ten individuals) that dispersed between trees was determined and used as the response variable for the weather correlation analysis. No individual snail used in this regression contributed more than one movement to the analysis, meaning 11 different individuals' movements appear in Table 2. There were 12 potential meteorological predictor variables including maxima (max), minima (min), and averages (avg) for the four weather parameters measured (% relative humidity [RH], temperature in degrees Celsius [T, °C], wind speed [m/s], and wind gust speed [m/s]). Maximum RH was always 100% and both minimum wind measures (speed and gust) were 0 m/s, and so these three predictors were not included.

Temporary weather station malfunctions, and site/month combinations in which all ten transponder snails were not relocated, were responsible for excluding 14 monthly records in the weather correlation analysis. Of 28 possible monthly records (four sites, 7 months), only 14 were actually used in this analysis (Table 2). Regrettably, all four weather stations needed sensor replacement at least once during this study due to corrosion. Snail-tag loss per month varied substantially between sites and seemed to reflect the relative exposure to inclement weather at each site. In decreasing order from least exposure to greatest are Kahanaha'iki, Palikea, Opae'ula, and Poamoho. The numbers of tags lost by site are summarized in Table 3. When even a single snail remained undetected for more than 1 month, further radar monitoring was terminated at that site because dispersal could no longer be distinguished from tag loss or death. For most months involving tag loss, a subsequent intensive search of the area (sometimes requiring an additional day in the field) recovered snails with broken transponders that could be fixed before the next sampling interval.

The best-subsets regression model that outperformed all other models (using Akaike's information criterion, Akaike 1974) for explaining variation in dispersal (Table 2) contained only two predictor variables: maximum wind gust speed and average RH ($R^2 = 0.77$, $p < 0.001$). The estimates of these coefficients were both positive and significant at $\alpha = 0.05$. Of the single predictor models, maximum wind gust speed performed best ($R^2 = 0.59$, $p = 0.0014$). RH was the next best of the single predictor models, but did not perform nearly as well ($R^2 = 0.43$, $p = 0.011$).

Discussion

The initial goals of this project were to determine the short-term dispersal rates of two species of *Achatinella* and the effects weather may have on those rates. Use of harmonic radar methods provided rough estimates of dispersal, which are often difficult to separate from mortality or recapture probability in CMR analyses. The weak correlation of dispersal with wind gusts during winter months suggests that between-tree movements might be mostly passive rather than active, and that members of *Achatinella* spp. are blown out of their trees during violent wind storms. These findings agree with observations from January 1985 in which many snails from a previous CMR study of *Achatinella mustelina* were found far

Table 1. Distance traveled by individual snails (in meters) by month that moved between trees, measured as the distance between tree bases. Non-zero values are boldfaced. ?, snail never relocated; NA, not applicable.

Snail ID code	Site	August	September	October	November	December	January	February	March
A2	Palikea	0	0	0	0	0	0	0	0
A5	Palikea	0	0	0	0	0	**3**	0	0
A7	Palikea	0	0	0	0	0	0	0	0
A8	Palikea	0	0	0	0	0	0	0	0
B1	Palikea	0	0	0	0	0	0	0	0
B8	Palikea	0	0	**5**	0	0	0	0	0
B9	Palikea	0	0	0	0	0	0	0	0
H2	Palikea	0	0	0	0	0	0	0	?
H7	Palikea	0	0	0	0	**4**	**2**	0	0
J0	Palikea	0	0	0	**7**	0	0	0	0
B2	Kahanaha'iki	0	0	0	0	0	0	0	
D4	Kahanaha'iki	0	0	0	**6**	**6**	0	?	
G0	Kahanaha'iki	0	0	0	0	0	0	0	
G6	Kahanaha'iki	0	0	0	0	0	0	0	
J7	Kahanaha'iki	0	0	0	0	0	0	0	
K2	Kahanaha'iki	0	0	0	0	0	0	0	
Q0	Kahanaha'iki	0	0	0	0	0	0	?	
Q9	Kahanaha'iki	0	0	0	0	0	0	?	
R0	Kahanaha'iki	0	0	0	**3**	0	**7**	0	
T0	Kahanaha'iki	0	0	0	0	0	0	?	
A3	Poamoho	NA	0	0	0				
D3	Poamoho	NA	**6**	0	0				
E4	Poamoho	NA	0	0	0				
E5	Poamoho	NA	0	0	0				
H1	Poamoho	NA	0	**4**	?				
H9	Poamoho	NA	0	0	0				
J3	Poamoho	NA	0	0	?				
K1	Poamoho	NA	0	**5**	?				
K5	Poamoho	NA	**3**	0	0				
Q3	Poamoho	NA	0	0	?				
A3	Opae'ula	0	0	0	0				
A5	Opae'ula	0	0	0	?				
L5	Opae'ula	0	0	0	0				
M6	Opae'ula	0	0	0	0				
N4	Opae'ula	0	0	0	?				
N9	Opae'ula	0	0	0	0				
Q1	Opae'ula	0	0	0	?				
Q4	Opae'ula	**6**	0	0	?				
R5	Opae'ula	0	0	**5**	**5**				
R6	Opae'ula	0	0	0	**7**				

away from their origins following hurricane force winds during a severe winter storm (M.G. Hadfield, unpubl. data).

In the present study, a radar helped to relocate snails in vegetation that is not normally thought to be a prime host for snails. A common morph of the native tree *Metrosideros polymorpha* has a fuzzy leaf texture, which is usually avoided based on observations of captive and wild snails (unpubl. data). However, at least two snails were relocated with a radar on this particular tree morph. Some transponder-equipped snails have also been recaptured in dense foliage and/or on high branches that would have been challenging to search thoroughly. Use of the radar alone resulted in recapture rates $\geq 80\%$ at every site, which is more than double that of equivalent effort with CMR (K.T. Hall, unpubl. data).

Except where mentioned earlier, all non-recaptures can be attributed to breaks in the transponders at weak solder bonds. Most of these non-recaptured

Table 2. Meteorological predictor variables corresponding to the number of dispersing snails for each site/month combination. avg., average; max., maximum; min., minimum; RH, relative humidity; T, temperature; WS, wind speed; WG, wind gust.

Site, month	Dispersed snails (no.)	T (°C) (max.)	T (°C) (avg.)	T (°C) (min.)	RH% (avg.)	RH% (min.)	WS (avg.)	WS (max.)	WG (avg.)	WG (max.)
Palikea, August	0	25.2	18.5	16.0	95.5	60.3	1.8	4.2	4.0	9.5
Palikea, September	0	22.9	18.1	16.0	97.2	69.8	2.0	5.0	4.4	8.8
Palikea, October	1	25.2	18.8	16.0	97.9	70.3	1.3	4.2	3.2	9.1
Palikea, November	1	25.2	18.1	15.6	99.6	74.8	1.9	6.1	4.1	11.4
Palikea, December	1	24.0	16.2	13.3	97.1	68.3	1.7	5.3	4.0	10.7
Palikea, Feburary	0	23.2	15.7	12.9	98.0	45.3	1.6	5.0	3.8	8.8
Kahanaha'iki, August	0	32.3	21.1	15.6	97.0	45.3	1.0	4.6	3.6	9.9
Kahanaha'iki, September	0	30.7	20.8	17.1	96.0	48.3	1.3	3.1	4.8	10.3
Kahanaha'iki, November	2	31.5	20.0	14.9	99.0	46.3	2.0	5.0	5.0	12.0
Poamoho, September	2	26.7	19.2	16.8	98.5	72.8	2.4	6.5	5.9	13.7
Poamoho, October	2	26.0	19.3	16.8	98.6	81.8	1.4	5.7	3.9	13.7
Opae'ula, August	1	27.1	19.1	14.1	96.7	47.8	1.8	4.2	5.3	10.7
Opae'ula, September	0	24.0	18.7	16.4	95.8	58.3	1.9	4.2	5.7	11.8
Opae'ula, October	1	26.7	18.9	14.5	96.2	60.8	1.3	5.0	4.2	11.8

snails were eventually seen again during intensive searches with only the diode still attached. This is the major limitation of the transponders. Larger, more durable tags were tested, but affected natural snail behavior. Snails would sometimes come to rest without fully retracting into their shells, while others would have movement restricted by rigid wire kinks. In order to determine the fate of snails with failed transponders, considerable time was required to locate those individuals. Sometimes, this necessitated another trip to a field site specifically to find a lost snail.

Table 3. Number of transponder tags lost per month per site. *Weather station malfunctions. **At least one transponder snail never recaptured. Cells containing values without asterisks are the same site/month combinations found in Table 2.

	Kahanaha'iki	Palikea	Opae'ula	Poamoho
August	0	1	0	
September	0	2	1	2
October	0*	2	2	2
November	0	1	4**	3**
December	2*	1		
January	2*	1*		
February	4**	2		
March		3**		

Non-detection of dispersal is very problematic for CMR studies and was a major reason why a radar was used in this study. Despite dramatic improvements in detection ability, harmonic radar methods in their current form still cannot entirely eliminate non-detection of dispersal. For tree snail studies in which inclement weather is not a substantial factor, this method should suffice for monitoring purposes. However, further transponder modifications will be needed in study areas that are prone to severe weather and/or where regular access is limited. J. Kiriazi (UH Mānoa Electrical Engineering Department) is currently assisting the authors of this article with ways to increase the durability of transponders through more conformal designs that are less prone to wear and tear as snails forage through thick vegetation. These designs cover more of the shell's surface area, reducing the need for an antenna extension beyond the length of the snail. In addition, we are exploring ways to create transponders with unique frequencies by changing the length of the antennae. These approaches require a different transmitter and receiver with an adjustable frequency, a function not available with the Recco unit.

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