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Human Dimensions of Wildlife Management Article

Modeling Harvest Intensity of Sooty Shearwater Chicks by Rakiura Māori in New Zealand

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ABSTRACT Cultural evidence suggests that sooty shearwater (*Puffinus griseus*) chicks have been harvested by Rakiura Māori on islands in southern New Zealand since prehistoric times. Concerns exist that modern harvests may be impacting sooty shearwater abundance. We modeled human-related and ecological determinants of harvest (total no. of individuals harvested) of sooty shearwater chicks on 11 islands and examined the relationship between shearwater abundance and harvesting rates (chicks/hr) and harvester behavior throughout the harvesting season. Models best explaining variation in harvest between harvesting areas (manu), for both the early and late parts of the harvesting season, included harvester-days (included in all models with change in deviance information criteria [ΔDIC], $\Delta\text{DIC} < 8.36$ and $\Delta\text{DIC} < 11.5$, for the early and late periods, respectively). Other harvest determinants included shearwater density, size of the manu, and number of people helping harvesters (all included in the top 5 models within $\Delta\text{DIC} = 2.25$ for the late period). Areas harvested by several families under a common-property harvesting system had higher harvest intensity for their size (24% points higher, 95% credible interval 11–36%) than those managed as an exclusive resource for one family. The slowest harvesters spent more time harvesting but on average only harvested 36% (95% credible interval 15–65%) and 34% (95% credible interval 12–63%) of the harvest taken by the fastest harvesters during the early and late periods, respectively. Our results highlight the possibility of elevated harvest intensity as the population of harvesters increases. However, our models suggested that a corresponding reduction in harvesting rate at low prey densities during the most productive period could potentially regulate harvest intensity. Future research will integrate these results into prospective shearwater demographic models to assess the utility of a range of harvesting strategies in ensuring harvest sustainability.

KEY WORDS common property, cultural harvest, functional response, harvesting rate, New Zealand, *Puffinus griseus*, regulation, sooty shearwater.

There is a long history of human exploitation of seabirds and many of these harvesting systems are ongoing (Feare 1978, Beatty 1992, Oka 1994, Baker et al. 2004, Moller 2006). However, despite the cultural and social importance to some societies (Wilson 1979, Beatty 1992, Oka 1994, Taiepa et al. 1997), the threatened status of several exploited species (Robertson 1991), and the vulnerable nature of seabird life histories to harvest in general (Saether and Bakke 2000, Hunter and Caswell 2005), few harvesting systems have been investigated quantitatively (Moller 2006).

Determining harvest intensity, the proportion of the effective target population that is harvested in a given time period, should be the first step when assessing sustainable use of a wildlife resource (Milner-Gulland and Ackakaya 2001, Sutherland 2001, Moller 2006). Harvest theory suggests that presence of compensatory mortality or natality is usually necessary for sustainable harvesting (Sutherland 2001). Estimates of harvest intensity are therefore essential for determining the negative feedback from density needed to reduce harvest impacts. Furthermore, temporal and spatial comparisons of abundance between harvested and unharvested populations could also be strengthened by using harvest intensity as a covariate in analyses (Moller 2006). To reliably predict future sustainability of the harvest it is essential to also understand determinants of harvest intensity. Integration of biological and human dimensions of harvesting systems is increasingly being promoted as an improved method of understanding and managing impacts of harvests (Branch et al. 2006, Ling and Milner-Gulland 2006). Risk assessment can then link scenarios involving future changes in socioeconomic conditions to fluctuations in determinants of harvest intensity.

Annual harvest of sooty shearwater (*Puffinus griseus*) chicks (muttonbirding) on islands in Foveaux Strait and around Stewart Island is one of the few remaining large-scale customary uses of native wildlife still practiced by New Zealand Māori today (Wilson 1979, Taiepa et al. 1997). The time period over which harvesting has occurred remains uncertain due to a lack of archaeological data, although harvesters' cultural knowledge suggests it may date back to prehistoric times (Hawke et al. 2003, Stevens 2006). However, there is currently concern that an increasing population of harvesters, easier access (i.e., more efficient boats and helicopters), and technological improvements in harvesting equipment, such as electric plucking machines, may have disrupted the dynamics of the harvesting system by increasing harvesting rates or total harvest (Lyver and Moller 1999, Moller 2006, Stevens 2006). The effect of these changes in harvest may be exacerbated by recent declines in sooty shearwater populations (Veit et al. 1997,

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Lyver et al. 1999, Scofield 2001, Scofield and Cristie 2002). Our overarching objective was to estimate current levels of harvest of sooty shearwater chicks by Rakiura Māori and increase our knowledge about the potential changes in harvest that will occur with future changes in harvester-related and ecological variables. Within this scope we aimed to identify the relationships between current harvest and a suite of predictor variables, determine the relationship between prey density and harvesting rate, and investigate whether harvesters have the ability to modify their current behavior (e.g., time worked per day) to maintain harvests in the face of declining shearwater numbers. Knowledge of these relationships is essential for future development of demographic models to identify optimal harvest strategies under current and future conditions. Our objective was to identify the relationships between harvest and variables likely to change as the population size of harvesters increases (e.g., no. of harvester-days). We hypothesized that harvest would be higher on harvesting areas (manu) with high harvesting effort, high chick densities, large area, low proportion of understory vegetation, and high numbers of people helping process the harvest and where multiple families harvest from a common area and where electric machines are used to pluck chicks. We aimed to determine the relationship between prey density and harvesting rate, which is generally assumed (often without testing) to be linear (Maunder et al. 2006). Linearity would suggest that harvesting rate could be a useful index of shearwater abundance in future monitoring schemes. We also examined the influence of harvesting rates on harvester behavior during the season. We tested whether harvesters with the fastest harvesting rates were able to obtain higher total harvests than slower harvesters or whether the increased processing time of higher harvest levels dampened their speed advantage. With each of these undertakings we sought to make inferences about the likely changes in harvest levels and harvest intensity that will occur in the future as populations of both humans and shearwaters change.

STUDY AREA

Thirty-six islands constituted the Tītī Islands in southern New Zealand, most of which were subjected to regular harvesting by Rakiura Māori (New Zealand's southernmost indigenous group). There were 3 main groups of islands: the southwestern, northeastern, and eastern groups (Fig. 1). Between 1999 and 2005, we surveyed 21 harvested manu (discrete harvesting areas) from 11 islands spread throughout the island groups (Fig. 1; Table 1). Research authority to survey harvested manu within the project was conditional on results remaining anonymous, so we refrained from linking measurements to identifiable individual manu. Two main forms of harvesting system existed on the islands. Most commonly, islands were split into well-defined sections (manu), each of which was harvested by an individual family (closely related individuals that operated out of one workhouse). Boundaries and family members visiting the manu were generally consistent among years.

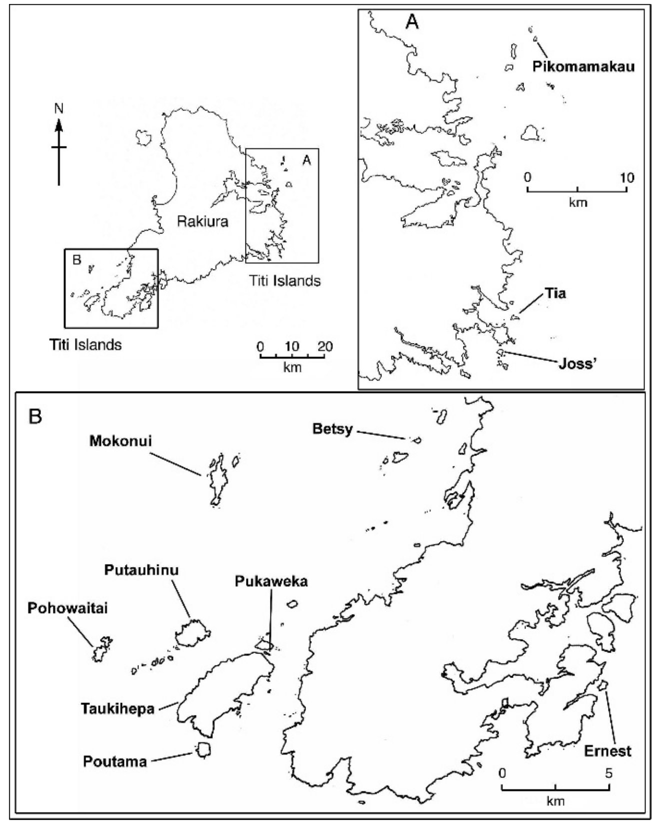


Figure 1. Location of the 11 islands around Rakiura (Stewart Island), southern New Zealand, where we assessed harvest of sooty shearwater chicks between 1999 and 2005. We surveyed multiple manu on several islands.

We defined these manu as closed ($n = 16$). On 5 islands distinct manu did not exist and several families harvested birds from anywhere on the island. We defined these as open manu. In open manu there was >1 workhouse on the island with a different family operating out of each workhouse (although in some cases these families were genetically related). Movements and harvesting by individual families were largely independent of each other. Several small islands supported only one family and so we considered each of these to be one closed manu.

Laws governing harvest of sooty shearwater chicks were formalized under the Tītī Islands regulations (New Zealand Government 1978). Many of the laws reflected the traditional knowledge that conserved the resource (Kitson and Moller 2008). For instance, the islands were ordained to remain uninhabited for most of the year, and access between 15 March and 31 May was only allowed by Rakiura Māori harvesters. This limited access prevented disturbance to breeding birds, especially during the sensitive period when adults were incubating eggs (Serventy and Curry 1984).

Two community-elected bodies (the Rakiura Tītī Islands Administering Body and the Rakiura Tītī Islands Committee) oversaw these laws and were preparing management plans and new bylaws for the islands (Kitson and Moller 2008). The harvest period consisted of 2 periods. The Nanao occurred in the early part of the season, from 1 April to approximately 20 April, when chicks were harvested from

Table 1. Area, harvesting system, and sampling design on the 21 manu (harvesting areas) on 11 islands in southern New Zealand where we surveyed harvesting of sooty shearwaters by Rakiura Māori between 1999 and 2005.

Island	Manu	Harvesting system	Area (ha)	No. of plots	No. of transects
A	1	Closed	2.1	120	12
B	2	Closed	2.7	144	12
C	3	Closed	9.3	174	15
D	4	Closed	5.7	168	14
E	5	Closed	7.7	170	10
F	6	Closed	10.3	144	12
G	7	Open	28.8	165	14
H[a]	8	Open	22.5	80[a]	38[a]
I	9	Open	4.5	167	14
I	10	Closed	2.6	180	11
J	11	Closed	12.1	252	12
J	12	Closed	13.9	242	12
J	13	Closed	14.5	238	12
J	14	Closed	16.5	269	12
J	15	Closed	15.6	259	11
K	16	Open	10.4	180	14
K	17	Closed	4.9	168	10
K	18	Closed	7.0	72	13
K	19	Closed	11.2	180	15
K	20	Open	27.3	164	14
K	21	Closed	5.8	192	12

[a] From Lyver 2000.

their burrows during daylight. The Rama occupied the remainder of the season when chicks emerged from burrows at night and harvesters used torches to catch them on the ground surface (Wilson 1979, Lyver 2002, Kitson 2004).

Chicks underwent processing when they were returned to the workhouse. Processing typically involved plucking feathers by hand or machine (Lyver and Moller 1999), applying wax to the plucked chick to remove remnant down, cutting and cleaning, salting, and finally, packaging for storage.

METHODS

Study Design

With the exception of Putauhinu Island, where our more intensive studies and long-term monitoring occurred, we surveyed each manu once between 2000 and 2005. During surveys we subdivided the manu into 3 to 15 strata. We established stratum of roughly equal (within manu) size based on features such as walking tracks, harvesting wires, and ridgelines that allowed us to easily mark strata boundaries. We randomly (using random number generators to select coordinates) placed circular plots with a 3-m radius (28.3-m^2 surface area) within each stratum to count burrow entrances. Number of plots sampled ranged between 8 and 48 plots, according to the size of the stratum (Table 1). We considered a burrow entrance to be any entrance from which ≥ 1 tunnel extended >20 cm and we defined burrow occupancy as number of chicks per burrow entrance (Lyver et al. 1998). On several islands low numbers of other small petrel species were present. These species generally occupied smaller burrow entrances, so we only included entrances that had a height and width each >8 cm, the minimum size that sooty shearwaters can enter (Scott 2005).

In addition, if time constraints allowed, we randomly established either 2 or 3 strip transects within each stratum for more intensive examination of burrow occupancy and to allow repeat monitoring in future breeding seasons. Density of burrow entrances varied among islands so transects of fixed length would have resulted in variable sample sizes of entrances, from which we would determine burrow occupancy. We adopted a more efficient approach that utilized transects where the sample size of burrows was fixed and transect length varied. We determined length of transects by extending a tape measure on a random bearing from the start point until 20 burrow entrances were included within the transect bounds, 1 m either side of the center line (2 m on 2 of the manu). We searched each of the 20 burrow entrances within the transect using an infrared burrow scope to determine the proportion of entrances occupied by chicks (burrow occupancy; Lyver et al. 1998). Our methods complied with the University of Otago animal ethics and human ethics regulations (permit no. F02/001).

Estimating Chick Numbers

A natural estimate of chick numbers (prior to harvesting) is

$$\hat{N} = \sum_i A_i e_i d_i$$

where A_i is area of stratum i, e_i is mean number of entrances/m^2 over all plots in stratum i, and d_i is mean number of chicks per entrance (burrow occupancy) over all transects in stratum i. However, monitoring sooty shearwater abundance using a burrow scope underestimates true number of occupants (McKechnie et al. 2007). Distance of burrow occupants from the burrow entrance is a strong predictor of their detection using the burrow scope, and corrections incorporating a detection function based on this burrow characteristic improve occupancy estimates. We calculated a manu-wide correction factor (k) for burrow scope bias as

$$\hat{k} = \frac{n}{\sum_x \frac{n_x}{\hat{g}(x)}}$$

where n was total number of chicks detected and n_x was number of chicks detected at distance x (measured using 10-cm intervals); we calculated both n and n_x over all transects within a manu. The function $\hat{g}(x)$ was estimated probability of detecting a chick that was at distance x from the burrow entrance, as McKechnie et al. (2007) defined as the linear logistic function

$$\hat{g} = \frac{1}{1 + \exp\{-(a + bx)\}}$$

where a and b were the intercept and slope terms, respectively.

We then calculated a detection-corrected estimate of chick numbers as

$$\hat{N}' = \hat{N}/\hat{k}.$$

We used measurements of slope from each transect to correct for any negative bias incurred when we relied on planar rather than surface estimates of area, assuming slope measurements on transects were representative of those over the whole manu. Our final estimate of number of chicks was

$$\hat{N}'' = \hat{N}'/b$$

where b was the mean over all transects of $b_j = \cos(\theta_j)$, and θ_j was slope measured on transect j using an inclinometer. We calculated chick density (chicks/m^2) as $\hat{c} = \hat{N}''/M$ where M was total area of the manu.

We established transects on 4 of the 5 harvested manu on Putauhinu Island in 1997 as part of a program to monitor changes in shearwater abundance on that island. We measured burrow occupancy on transects in the 1997–1999 and 2003–2005 breeding seasons. Because these data only provided information about relative changes in abundance, we also surveyed total population size on each manu on Putauhinu Island (in one season only, with season varying between manu) using methods described above for the other islands. We included data on total population size for 2 manu. However, harvesting data were not available for the remaining 2 manu in the season that we surveyed total population size, so for 2 manu we used information on relative changes in abundance on the transects to estimate population size in a season when harvesting information was available (Bragg et al. 2009). We surveyed population size of the single remaining harvested manu on Putauhinu in 2005. We also added data from Poutama Island, which was surveyed in 1994 and reported by Lyver (2000) to the set, giving 21 manu on 11 islands.

Estimating Harvest Intensity

Harvesters recorded number of chicks taken from each manu every year (i.e., harvest). Harvesting rate was harvest per unit time. Harvesters also recorded harvests for every day and time spent hunting on standard data forms while researchers were present on the island and thus we could verify accuracy by inspecting number of chicks processed and comparing this to recorded data. We observed no discrepancies. We estimated harvest intensity (i.e., proportion of chicks available that are harvested) as

$$\hat{h} = \frac{T}{\hat{N}''}$$

where T was total harvest of chicks by all harvesters on the manu and $\hat{N}''$ was number of chicks on the manu just prior to harvesting. We calculated harvesting rate (i.e., chicks/hr) when harvesters recorded amount of time spent catching chicks, generally for each day of the season. Daily (or nightly during the Rama) we summarized harvesting rates for the Nanao and Rama separately as

$$\hat{f}_i = \frac{T_i}{t_i}$$

where t was total number of hours spent hunting by all harvesters on the ith day or night of the Nanao or Rama period, respectively.

We calculated time from when processing of chicks harvested on the manu began until the last chick was processed, P (hr), as

$$\hat{P} = \frac{TX}{H + H'}$$

where H was number of harvesters operating, H' was number of helpers involved in processing, and X was mean time (0.03 hr) taken to process harvested chicks into the packaged product, as measured by Lyver and Moller (1999). Processing of chicks typically begins once the entire harvest is procured, and harvesters and helpers generally perform similar tasks during processing and hence receive equal weighting in the denominator.

Statistical Analyses

Although our objective was to determine predictors of harvest intensity from a suite of potential explanatory variables, several of these variables (e.g., chick density and area) are utilized in calculation of N, and hence would occur on both sides of the regression equation if we used harvest intensity as a response variable, leading to complications in the analysis. We therefore investigated the relationship between harvest on the manu and models containing up to 7 of the following explanatory variables (Table 2): 1) harvester-days: number of people-days spent harvesting (does not include helpers) on the manu during the season, 2) area: surface area of the manu, 3) chick density: density of chicks on the manu, 4) helpers: number of people that helped transport and process but did not themselves harvest chicks, 5) plucker: whether an electrical plucking machine was utilized, 6) vegetation: proportion of the manu covered by understory vegetation, and 7) management: whether the manu was an open or closed harvesting system.

We used a Bayesian approach to model selection to determine the model (or models) best supported by the data (Gelman et al. 1995). We established a candidate model set

Table 2. Descriptions of explanatory variables we used to model variation in number of sooty shearwater chicks harvested by Rakiura Māori on islands in southern New Zealand between 1999 and 2005.

Variable	Notation	Description	Unit	Hypothesized relationship with harvest
Harvester-days	P	No. of people-days spent harvesting (harvesters only and does not include helpers) on the manu during the season	Count (ln transformed)	More harvesters allows higher harvest per manu
Area	A	Surface area estimate of the manu	m^2 (ln transformed)	Larger manu allow harvesters to focus on more productive areas with higher catch rates
Chick density	C	Mean density of chicks on the manu	Chicks/m^2	Higher densities allow higher catch rates
Helpers	H	No. of people involved in helping harvesters transport and process the catch but that do not harvest chicks themselves. Helping includes activities such as carrying, cleaning, and packaging of chicks.	Count	If the harvest is limited by the time it takes to process chicks additional helpers will speed this phase up and allow increased harvest
Plucker	K	Whether an electrical machine was utilized when plucking down and feathers from harvested chicks (instead of hand plucking) on the manu	Binary	Machine pluckers allow more efficient processing of chicks
Vegetation	V	Proportion surface area of the manu covered by understory vegetation below chest ht	Proportion	A high proportion of ground cover restricts area of manu available for harvesting chicks
Management	M	Open manu are those in which the harvesting area is common property amongst ≥ 2 discrete harvesting groups. Closed manu are those in which one group harvests.	Binary	Open manu act as a common property resource where competition for chicks leads to lower incentives for conservation and hence higher harvest

a priori by excluding those models that were not biologically realistic (Burnham and Anderson 2002). We only included helpers and pluckers in models that contained harvesters, because it is difficult to conceive of a scenario where number of helpers on a manu could have more influence on harvest than number of harvesters actually harvesting chicks. Furthermore, advantages of using plucking machines in previous studies certainly did not approach levels equivalent to increases in harvester effort (Lyver and Moller 1999, Kitson 2002). We only included vegetation in models that contained area because we hypothesized vegetation (Table 2) to negatively influence harvest by restricting area searched by harvesters hunting chicks. We natural-log transformed the explanatory variables harvester-days and area to ensure linearity of relationships (Zar 1999). Our resulting candidate model set consisted of 45 models. We analyzed 2 response variables: harvest in the Nanao and harvest in the Rama. We also refitted the Rama models after we recalculated chick density by removing chicks harvested during the Nanao from number available. Parameter estimates were similar to the original model due to the low number of chicks taken during the Nanao. We do not present these refitted, recalculated results, because future use of parameter estimates will generally estimate harvest from chick densities measured before the Nanao harvest takes place.

We fitted a multilevel model to the data using Markov chain Monte Carlo (MCMC) simulation in WinBUGS 1.4 (Lunn et al. 2000). The data were structured such that we had observations from $i = 1,\ldots, n$ manu nested within islands $j = 1,\ldots, J$. The model contained a coefficient for the constant term α that varied between islands, that is,

$$y_{ij} = \alpha_{j[i]} + X_i\beta + \varepsilon_i$$

where X was a vector of the various explanatory variables, β was a vector of the individual-level regression coefficients, and ε was the individual-level error term (i.e., $\varepsilon \sim Normal\left(0, \sigma_\varepsilon^2\right)$ with the constant term further modeled as

$$\alpha_i \sim Normal\left(\mu_\alpha, \sigma_\alpha^2\right).$$

We used non-informative normal priors ($\sim$ *Normal*[0, 10,000]) for the individual-level coefficients β and mean of the constant term μ_α, and we used non-informative uniform priors ($\sim$ *Uniform*[0, 100]) for the standard deviation terms σ_t and σ_α (Gelman and Hill 2006). We ran the MCMC algorithm with 5 chains and monitored the Brooks–Gelman–Rubin diagnostic (Brooks and Gelman 1998) to ensure that all samples before convergence were discarded. We ran a burn-in phase of 30,000 iterations followed by 70,000 iterations from which we estimated parameters.

We ranked models using the Deviance Information Criterion (DIC), which is a generalization of Akaike's Information Criterion (AIC) more suitable for multilevel models (Spiegelhalter et al. 2002), calculated as

$$\mathrm{DIC} = \bar{D} + p_D$$

where $\bar{D}$ was posterior mean of the deviance calculated using the usual formula $-2 \log p\,(y|\theta)$ and was a measure of how well the model fit the data, whereas p_D was a measure of the effective number of parameters and thus complexity of the model. Hence, better models have lower DIC values.

We used the approach of Gelman and Pardoe (2006) to estimate the proportion of variance explained at each level of the model as

$$R^2 = 1 - \frac{E\left(V_{k=1}^{K}\varepsilon_k\right)}{E\left(V_{k=1}^{K}\theta_k\right)}$$

where E was the posterior mean, ε_k were the residual errors, and θ_k were the data points in the first level of the model and regression coefficients at higher levels. Because our model only had a constant predictor at the group (second) level, proportion of variation explained at this level will always be zero; hence, providing proportion of variation explained at the data (first) level sufficed in our case. Note that this measure had a similar interpretation to the classical adjusted R^2, and similarly could give negative values for poorly fitting models if the estimated error variance was greater than the data variance (Gelman and Pardoe 2006).

We constructed similar models with harvest intensity as the response and area and area per harvester as explanatory variables in separate models. We investigated quadratic relationships between the explanatory and response variables when suggested by data.

We fitted seasonal functional responses for the Nanao and Rama datasets separately, using average seasonal harvesting rate as the response and the same multilevel data structure as for the earlier analyses. We added chick density, measured on the manu prior to harvesting, as an explanatory variable. We calculated average harvesting rate (chicks harvested/hr) as

$$\bar{f} = \frac{1}{n}\sum_{i=1}^{n}\hat{f}_i$$

where $\hat{f}_i$ was estimated daily harvesting rate and i = 1 is 20 April and i = n is 18 May (the first and last days of harvesting, respectively, observed on any manu during the Rama). Daily harvesting rate during the Rama was dependent in a curvilinear relationship on day of the season (Fig. 2) whereby harvesting rate was lowest early and late in the Rama period and peaked roughly mid-season (Lyver et al. 1999). Because harvesting on some manu only occurred during parts of the Rama period it was difficult to calculate an average harvesting rate that is comparable across manu. For instance, if harvesters were only present on a manu during the middle of the Rama period, when harvesting rates were known to be higher than early or late in the period, then a raw average harvesting rate calculated across actual days harvested would be biased high relative to harvesters on another manu that were present for the whole period. Our aim was to compare the relationship between density of chicks and harvesting rate across manu, so we needed a method to standardize harvesting rate when harvest occurred across different periods of the Rama. We fitted a multilevel model to daily harvesting rate $\hat{f}_i$ (natural-log transformed), with day of season added as a fixed effect. We considered days on which no harvesting occurred on a given manu as missing values, which, when explicitly added to the model formulation in WinBUGS, were automatically estimated for each MCMC iteration during model fitting (Gelman and Hill 2006). We then

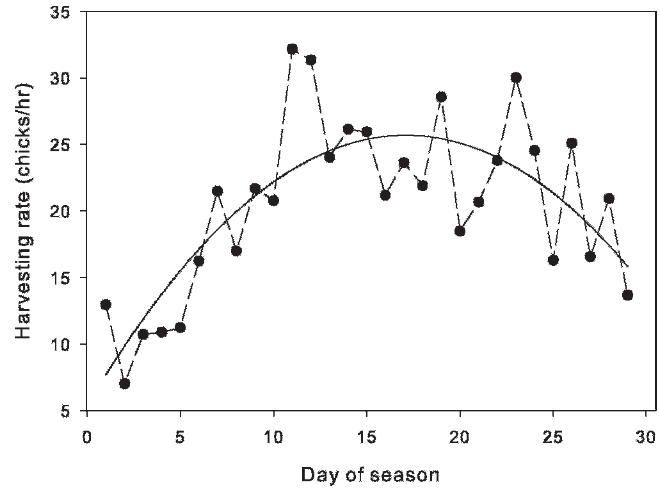


Figure 2. Observed and predicted harvesting rates of sooty shearwater chicks (chicks/hr) by Rakiura Māori over the Rama period (20 Apr [day 0] to 18 May [day 29]) of the harvesting season in southern New Zealand between 1999 and 2005. We calculated predicted means by fitting a multilevel model to the data to account for individual manu nested within islands, with day of season included in the model.

included these imputed missing values in the calculation of average harvesting rate on those manu where harvesting did not occur throughout the whole harvesting season. This adjustment for missing values was only appropriate for investigating the relationship between harvesting rate and chick density and did not apply to our estimates of number of chicks harvested (harvest) or harvest intensity on a manu. Daily harvesting rate during the Nanao appeared to be independent of day of the harvesting season, so there was no need to predict missing values when calculating average harvesting rate over this period (Kitson 2004). Unless otherwise stated, all intervals presented are Bayesian 95% credible intervals relating to the interval between the 2.5th and 97.5th percentiles of the posterior distribution.

RESULTS

Harvest Intensity

There was considerable variation between manu for most harvesting parameters. A median of 2,922 (interquartile range = 4,137, n = 21) chicks were harvested per manu over the harvest season (Table 3). When harvesting occurred during both periods on a manu, 79.5% (SD = 14.0, n = 14) of the harvest occurred during the Rama (median chicks harvested = 2,754, interquartile range = 3,231 chicks, n = 20), with fewer chicks taken during the Nanao (median chicks harvested = 554, interquartile range = 617 chicks, n = 14). This harvest resulted in a median of 17.9% of available chicks harvested (interquartile range = 14.0%, n = 21), although harvest varied between 4.9% and 54.1%.

Between 1 and 11 harvesters were present on a given manu during the harvest season, resulting in between 19 and 330 (median = 67, interquartile range = 80, n = 21) harvester-days of harvesting (Table 3). More effort was expended during the Rama when both periods were harvested on a manu ($\bar{x}$ = 71.9% of harvester-days occurred during the Rama, SD = 15.3%, n = 15), with a median of 27

Table 3. Parameters describing harvest of sooty shearwaters, harvest intensity, and human harvesting effort on islands in southern New Zealand between 1999 and 2005.

Variable	n	$\bar{x}$	Median	Lower quartile	Upper quartile	Interquartile range
Harvest						
Nanao	14	982	554	387	1,004	617
Rama	20	3,959	2,754	1,677	4,907	3,231
Total	21	5,416	2,922	1,873	6,010	4,137
% of chicks harvested						
Nanao	14	3.0	2.4	1.2	4.3	3.1
Rama	20	16.7	13.3	7.2	21.1	13.9
Total	21	20.0	17.9	12.3	26.4	14.0
No. of people						
Nanao	15	2.6	2.0	1.0	2.9	1.9
Rama	21	3.9	3.0	1.4	4.8	3.3
Harvester-days						
Nanao	15	29.9	27.0	13.5	36.5	23.0
Rama	21	76.8	54.0	32	91	59.0

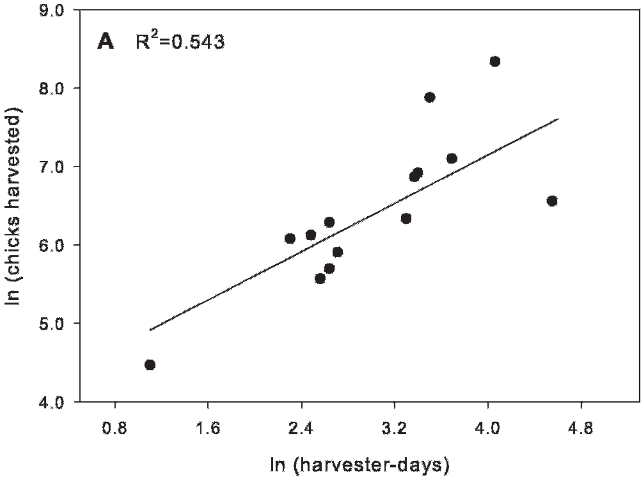
(interquartile range = 23, n = 15) and 54 (interquartile range = 59, n = 21) harvester-days harvested during the Nanao and Rama, respectively.

Determinants of Harvest

The model best explaining number of chicks harvested on a manu over the Nanao period included only one variable: harvester-days (Table 4), which showed a strong positive relationship with harvest (median regression coeff. β = 0.770, 0.261–1.280; Figs. 3, 4). This simple model fit the data better than the null model (R^2 = 0.543; Table 4). Harvester-days were also present in all other high-ranking models. Furthermore, variation in parameter estimates of the other explanatory variables (credible intervals for all

Table 4. Candidate models explaining variation in number of sooty shearwater chicks harvested by Rakiura Māori on islands in southern New Zealand during the Nanao and Rama harvesting periods between 1999 and 2005. We present models within a truncated candidate set that only includes models with Deviance Information Criterion (DIC) values <4 units higher than that of the best model. Also shown are the global and null models. Effective number of parameters estimated in each model is pD, the posterior mean of the deviance is $\bar{D}$, the change in DIC between the model and the best model is ΔDIC, and R^2 is the proportion of variation explained by the model. Model names indicate the variables included in that model, P: number of people-days harvesting on the manu, C: mean density of chicks on the manu, A: surface area of the manu, M: harvest management system on the manu, H: number of people helping the harvesters on the manu, K: whether an electrical plucking machine was utilized on the manu, and V: proportion of the manu covered by understory vegetation.

Model	Ranking	$\bar{D}$	pD	DIC	ΔDIC	R^2
Nanao						
P	1	23.44	3.87	27.31		0.543
P + C	2	23.27	4.83	28.10	0.797	0.537
P + A	3	23.88	4.61	28.49	1.185	0.515
P + M	4	23.94	4.60	28.55	1.241	0.513
P + H + K	5	23.40	5.38	28.78	1.477	0.521
P + A + C	6	24.00	5.41	29.41	2.101	0.497
P + H	7	24.85	4.73	29.58	2.279	0.480
P + C + M	8	24.96	5.57	30.53	3.221	0.457
P + C + H + K	9	24.34	6.23	30.58	3.270	0.467
P + C + H	10	25.21	5.64	30.84	3.538	0.453
P + A + M	11	25.55	5.40	30.95	3.65	0.443
P + H + M	12	25.64	5.38	31.02	3.71	0.421
P + A + H	13	25.65	5.40	31.05	3.710	0.440
P + A + C + V	14	24.94	6.36	31.30	3.996	0.432
Global	33	29.82	6.41	36.23	8.927	−0.235
Null	32	32.21	3.60	35.82	8.511	0.110
Rama						
P + A + C + H	1	17.00	7.30	24.29		0.815
P + A + C + H + V	2	16.35	8.42	24.77	0.481	0.818
P + A + C + H + V + M	3	16.79	9.53	26.32	2.023	0.809
P + A + C + H + M	4	17.94	8.43	26.37	2.078	0.804
P + A + C + H + K	5	18.60	8.12	26.72	2.425	0.798
P + A + H + V	6	19.06	7.79	26.85	2.553	0.794
P + A + H	7	20.72	6.65	27.36	3.068	0.779
P + A + C + H + V + K	8	18.28	9.32	27.60	3.308	0.800
P + A	9	22.15	6.12	28.27	3.972	0.763
Global	12	18.69	10.31	29.00	4.704	0.789
Null	45	47.64	5.11	52.75	28.461	0.151



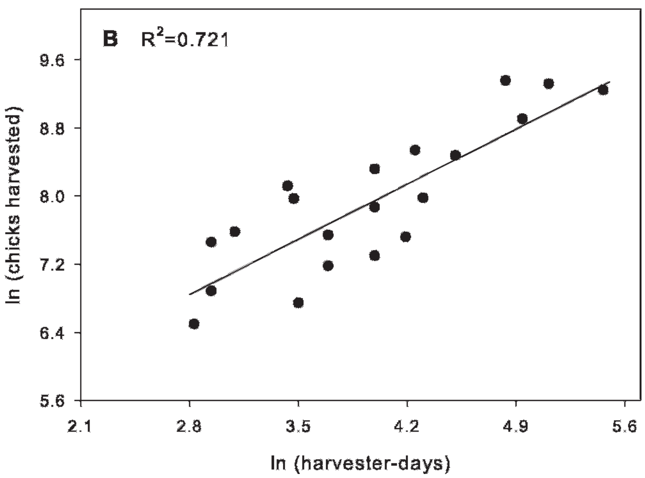


Figure 3. Relationship between harvester-days spent harvesting on a manu and number of sooty shearwater chicks harvested (both natural-log transformed) by Rakiura Māori during (A) Nanao period (1 Apr–approx. 20 Apr) and (B) Rama period (approx. 20 Apr–mid-May), in southern New Zealand between 1999 and 2005. The regression line represents predictions from models including only the explanatory variable harvester-days, which corresponds to the best-ranked model during the Nanao period but only the 20th-ranked model in the Rama period.

other variables included zero; Fig. 4) and the discrepancy between the direction of relationships we observed and those predicted (e.g., area; Table 2; Fig. 4) suggested that these variables were far less important in predicting harvest than was harvester-days.

Data collected during the Rama supported more complicated models than data collected during the Nanao (Table 4). The model best explaining variation in chicks harvested fit the data well (R^2 = 0.815) and indicated positive relationships between harvest and harvester-days, area, chick density, and helpers. Harvester-days were again estimated with the most precision (median β = 0.668, 0.353–0.986), although credible intervals for area (median β = 0.538, 0.145–0.923) and helpers (median β = 0.265, 0.033–0.498) also excluded zero (Fig. 5). There was more uncertainty in the estimate of effects of chick density (median β = 1.714, −0.132 to 3.552). Although the 3 explanatory variables of vegetation, plucker, and management occasionally occurred in high-ranking models, the 4 variables present in the best model (i.e., harvester-days, area, chick density, and helpers) were consistently present in the other high-ranking models (up until the fifth-ranked model), suggesting that these 4 variables were the most important determinants of harvest. The importance of these 4 variables is further supported by the high variation in parameter estimates for vegetation, plucker, and management. Harvester-days, area, and helpers were present in each of the top 8 ranking models.

There was a generally negative relationship between area and harvest intensity across all manu (Fig. 6A), although 4 manu appeared to deviate from the expected relationship. Each of these 4 manu occurred under an open harvesting system and only one other open manu appeared to approach the harvest intensity value that would be expected for its size under a closed system. A multilevel model with area and harvesting system as explanatory variables fit the data well (R^2 = 0.517; Fig. 6A). Part of this difference between harvesting systems can probably be attributed to a tendency for a higher number of harvester-days per unit area on open manu (median = 10.0×10^{-5} harvester-days/m^2, interquartile range = 6.7×10^{-5} harvester-days/m^2) than on closed manu (median = 6.9×10^{-5} harvester-days/m^2, interquartile range = 6.9×10^{-5} harvester-days/m^2). When considering the relationship between harvest intensity and area per harvester, deviations were in most cases reduced, producing a curvilinear relationship (Fig. 6B). A multilevel model with a quadratic relationship between harvest intensity and area per harvester fit the data adequately (R^2 = 0.512) and was an improvement on a model with a linear relationship (ΔDIC = 0.427). Examination of the residuals of the latter model also suggested this quadratic relationship was more suitable. The model suggested harvest intensity diminished quickly up until about 60,000 m^2 per person, but stabilized, and increased slightly, beyond this point.

Harvesting Rate and Harvester Behavior

We were unable to detect a relationship between density of chicks prior to the harvest and mean harvesting rate during the Nanao (median β = 4.03, −27.40 to 35.56). However, harvesting rate during the Rama showed a strong linear relationship with chick density (Fig. 7). The intercept of this equation was close to zero (median α = −5.61, −16.03 to 6.56), and the slope of the relationship (median β = 113.41, 71.89–139.80) suggested harvesting rate may be proportional to chick density.

There appeared to be no general relationship between Nanao harvesting rate and time actively catching per day (Fig. 8A). We detected a weak negative relationship between Rama harvesting rate and time catching per day during this period, with harvesters taking chicks at the fastest rate spending about 39% of the time that the slowest harvesters spent actively catching (Fig. 8B), although there was variation in the slope coefficient (median β = −1.16, −1.91 to −0.26).

During both harvesting periods, increased harvesting rate translated into increased harvest per day (Fig. 8C, D).

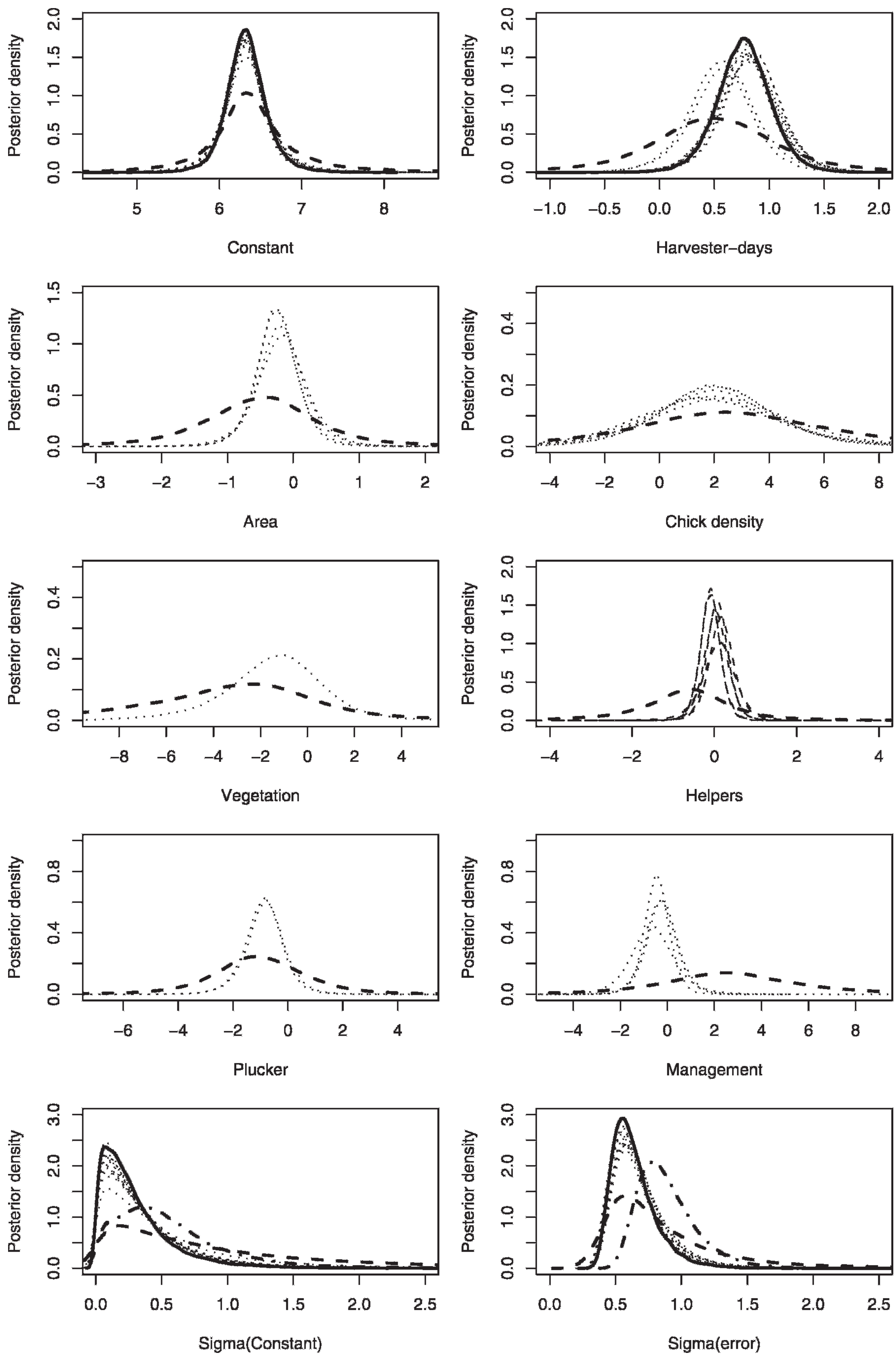


Figure 4. Posterior densities of parameters estimated in models predicting variation in harvest of sooty shearwater chicks by Rakiura Māori during the Nanao period (1 Apr–approx. 20 Apr) in southern New Zealand between 1999 and 2005. Separate lines represent estimated densities from different models. Estimates are displayed for all models with change in Deviance Information Criterion <4 higher than the best model. Densities for the best, global, and null models are represented by the solid, dashed, and dot-dashed lines, respectively. All other models are represented by dotted lines.

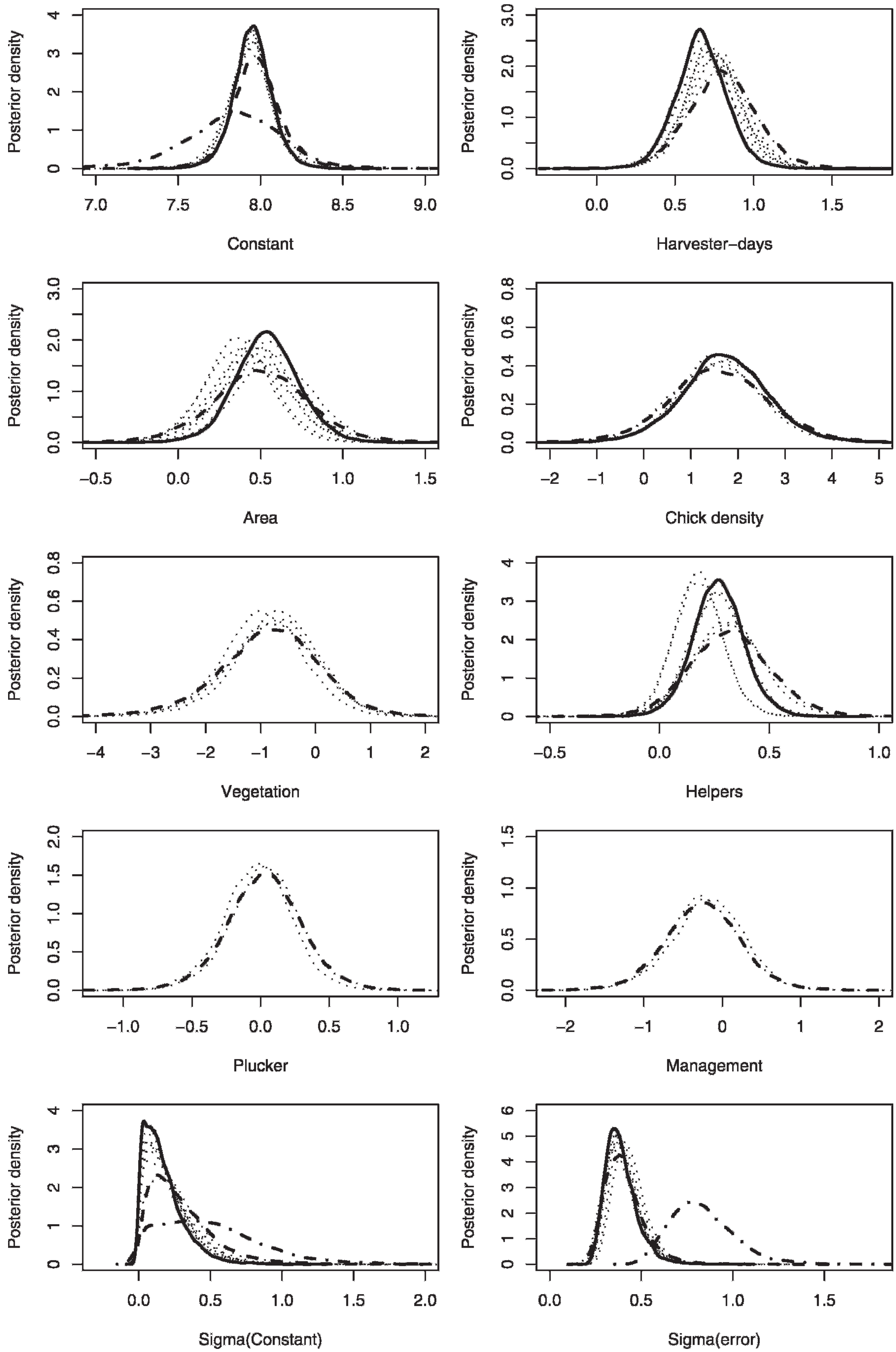


Figure 5. Posterior densities of parameters estimated in models predicting variation in harvest of sooty shearwater chicks by Rakiura Māori during the Rama period (approx. 20 Apr–mid-May) in southern New Zealand between 1999 and 2005. Separate lines represent estimated densities from different models. Estimates are displayed for all models with change in Deviance Information Criterion <4 higher than the best model. Densities for the best, global, and null models are represented by the solid, dashed, and dot-dashed lines, respectively. All other models are represented by dotted lines.

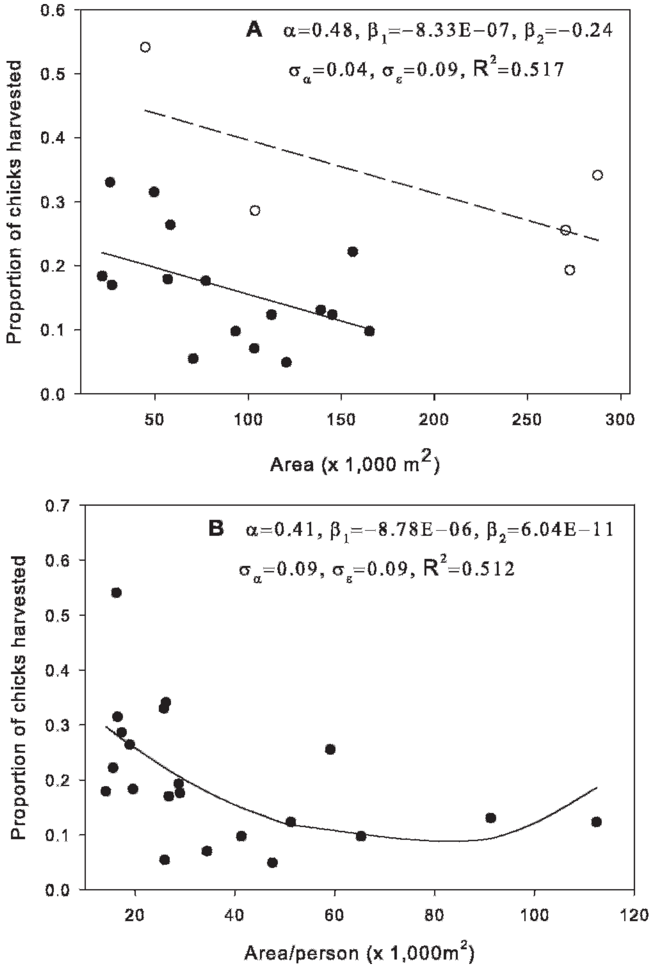


Figure 6. Relationships between (A) area of manu and (B) area of manu per person and proportion of available sooty shearwater chicks harvested by Rakiura Māori in southern New Zealand between 1999 and 2005. Solid and open circles represent manu with closed and open harvesting systems, respectively. Coefficients β_1 and β_2 correspond to (A) effects of area of manu and additive effects of open manu, respectively, and (B) linear effects of area per harvester and the quadratic effects of area per harvester, respectively. All parameter estimates displayed are medians of the estimated posterior distribution.

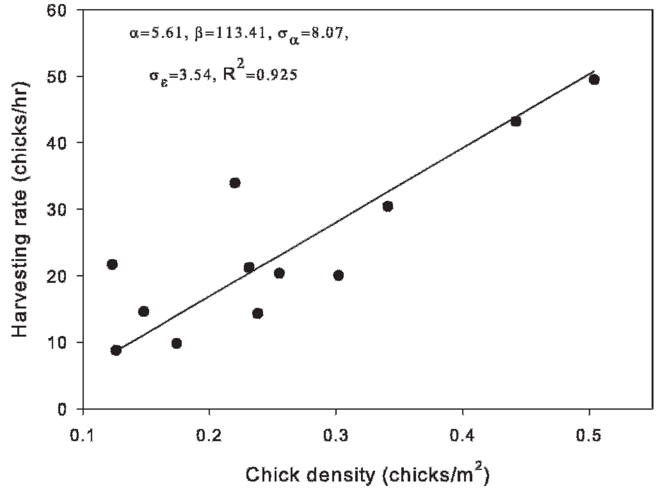


Figure 7. Relationship between density of sooty shearwater chicks on the manu prior to harvesting and harvesting rate (chicks/hr) by Rakiura Māori during Rama period (approx. 20 Apr–mid-May), in southern New Zealand between 1999 and 2005. All parameter estimates displayed are medians of the estimated posterior distribution.

However, there was substantial variation around the relationship during the Nanao (median β = 3.73, 1.60–5.80), with harvesters with the slowest harvesting rates taking 36% (15–65%) of the tally achieved by harvesters with the fastest rates. We observed a similar relationship during the Rama (median β = 36.64, 16.22–56.43) when harvesters with the slowest harvesting rates were taking just 34% (12–63%) of the tally achieved by harvesters with the fastest rates. Some of the unexplained variation is presumably due to the tendency of some harvesters to compensate for their reduced harvesting rate by increasing time spent catching, at least during the Rama (Fig. 8A, B). Despite less time spent catching during the Rama by harvesters with the fastest harvesting rates, the resultant increase in take, and hence processing time, offset the benefits. Thus there was no discernable relationship between harvesting rates and the amount of time spent working per day during either time period (Fig. 8E, F). Total daily work effort was higher during the Nanao ($\bar{x}$ = 6.13 hr, SD = 1.78) than during the Rama period ($\bar{x}$ = 4.88 hr, SD = 1.66), although there was considerable variation during both periods.

DISCUSSION

The only estimates other than ours of harvest intensity of sooty shearwater chicks are 17% and 23% on Poutama Island in 1994 and 1995, respectively (Lyver 2000). Although we included the 1994 estimate in our data set, these rates appear to be consistent with many of the other islands and straddle the median value we estimated (18%) and are certainly well within our observed ranges (5–54%). Estimating impacts of this magnitude of harvest requires development of sooty shearwater demographic models and is part of ongoing research.

Models explaining variation in harvest of chicks in both the Nanao and Rama periods always contained the variable of harvester-days. During the Rama there was also strong evidence that area, chick density, and helpers influenced harvesting. Prediction of harvest on unsurveyed manu would appear to be best undertaken with these simple models. However, the small sample size of manu we surveyed affected precision of several of these parameters. Therefore, collection of data from additional manu would not only allow validation of the current models but would also improve predictive precision.

Despite area being a weaker predictor of harvest than harvesting effort, it still strongly influenced overall harvest intensity. Spacing behavior of harvesters, as suggested by the positive correlation between harvester-days and manu area and the strong positive linear relationship between harvester effort and harvest, resulted in a largely regular harvest per unit area of manu. Consequently, as manu size, and thus chick numbers increased, harvest intensity decreased. The slight increase in harvest intensity on the largest of manu

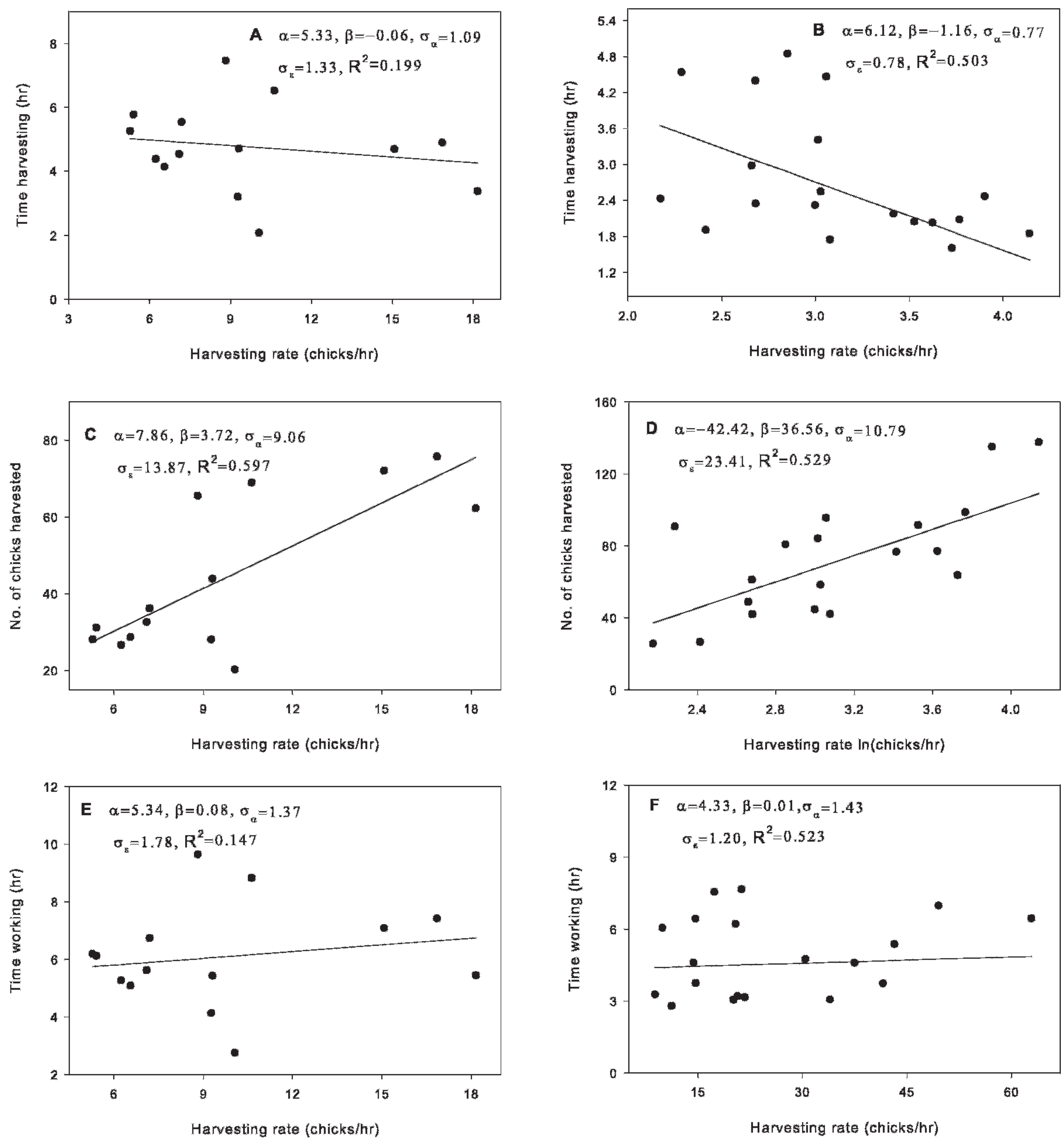


Figure 8. Relationship between harvesting rate of sooty shearwater chicks (chicks/hr) and (A, B) time spent harvesting (hr), (C, D) harvest, and (E, F) total time spent working (harvesting and processing chicks [hr]) by Rakiura Māori during the (A, C, E) Nanao (1 Apr–approx. 20 May) and (B, D, F) Rama (approx. 20 Apr–mid-May) periods in southern New Zealand between 1999 and 2005. All parameter estimates displayed are medians of the estimated posterior distribution.

may be related to harvesters there being able to spend most of their harvesting time in the most productive regions and therefore taking a higher harvest per area.

Those manu managed under open harvesting systems exhibited higher harvest intensities per unit area than those managed as closed systems. Reasons for these higher harvest intensities are unclear but are probably partly due to more effort being expended on open manu. Differences in exploitation rates between common property and privately owned resources often occur in human resource use systems, and the tragedy of the commons asserts that closure is a necessary condition for conservation of the resource (Hardin 1968, Ostrom et al. 2002). It is possible that incentives for restricting harvest for future use are lower on open manu where future unknown harvesters would benefit from curtailment of current harvest intensity, as predicted by theory (regulation of harvest on a given manu is determined by the harvesters present there rather than by higher authorities). Alternatively, the open manu convention may have been instigated on such areas precisely because more harvesters had access. If so, it may not have been the open area convention per se that triggered higher harvest intensity, but rather the higher number of people attracted to that manu. Harvesters on closed manu, however, may be restricting the number of harvesters present on the manu based on its size, thus limiting harvesting effort per unit area of manu. Research into the history of formation of open manu and the basis for regulation of the number of harvesters on a manu is necessary to evaluate these hypotheses.

From a management perspective harvest intensities can therefore be estimated by examining the relationship between harvest intensity and area of manu available per person. Based on hypothetical target intensities of 10%, 20%, and 30%, the optimal area per person would be about 60,000 m^2, 30,000 m^2, and 14,000 m^2, respectively (Fig. 6B).

We found no evidence relating chick density and mean harvesting rate in the Nanao. Harvesting chicks during the Nanao takes considerably more skill than during the Rama, so our results may have been influenced by variation in experience and skill between manu, matters for which we could not control in our study design. Further manu-specific differences in habitat such as burrow morphology and proximity of chicks to burrow entrances may have influenced our results. A more robust, though logistically demanding, approach would involve investigation of the relationship at a smaller spatial scale and thorough temporal monitoring of harvesting rates of a constant set of individuals. However, equivocal results for presence of a functional response during the Nanao have been reported previously by Lyver (2000) and Kitson (2004). In both studies, variation in harvesting rate of individual harvesters was investigated spatially within one island, suggesting that even at this scale, Nanao harvesting rate is difficult to predict.

In contrast, we detected a strong linear functional response between mean Rama harvesting rate and chick density. The increased importance of chick density in determining harvesting rate during the Rama corroborates the greater support for models that contained this variable when predicting harvest during this period. The regression equation passed through the y-axis close to the origin and predicted that for a change in chick density of $1/m^2$, harvest will increase by about 113 chicks ($y = 5.61 + 113.41x$). We found no evidence in the data for a deviation from linearity, as would be expected under alternative hypotheses of functional responses and as has been exhibited in several other harvesting situations (Hone 1990, Caley and Ottley 1995, Choquenot et al. 1999). This linearity suggests that either chick densities over the range we measured failed to reach levels necessary for saturation of harvest or that the time period over which we summarized the data did not allow us to detect nonlinearity. Number of chicks available for harvesting on a given night during the Rama is presumably determined by number of chicks emerging to exercise or fledge and not by absolute chick density estimated prior to the harvesting season, as we assumed. Emergence is variable between nights and is determined by several factors, such as chick development, wind, rain, and lunar activity (Lyver 2002).

Numbers of chicks emerging on several islands under certain conditions (Lyver 2002), coupled with high harvesting rates we observed on individual nights within a season, suggest that an upper bound on harvest is likely, at least on nights when conditions are optimal for emergence. It seems probable that the shape of the functional response at the individual night level is different from that at the season level although additional data, and modeling, are needed for confirmation.

Mean harvesting rates summarized over the Rama period appear to have utility in predicting chick density, at least at the manu scale. Thus use of this index is a cost-effective tool for monitoring resource management in a manner easily interpretable by the harvesters themselves (Lyver et al. 1999, Kitson 2004, Moller et al. 2004).

Our data provides both encouraging and discouraging prospects for future impacts of the sooty shearwater chick harvest. The major predictor of harvest, and hence harvest intensity, is number and effort of harvesters exploiting a given area. The strong correlation between area and harvester-days harvesting on the manu suggests that some form of spacing behavior is currently occurring, although the consequences of an increasing harvesting community remains to be seen. Under the Tītī Islands regulations (New Zealand Government 1978) any Rakiura Māori descendent can exercise the right to harvest birds on at least some islands, so there is the potential for steady increases in harvester populations as the number of people with harvesting rights increases almost exponentially. However, there is ample evidence in our data for negative feedback between chick density and harvest.

Firstly, there is a trend toward focusing harvesting on only the most productive period of the season (Kitson 2004). On many of the manu we surveyed, harvesters abstained from harvesting during the early part of the season, instead arriving just prior to or during the Rama period. Many harvesters attribute this behavior to a reduction in sooty shearwater abundance preventing profitable catches during less productive periods of the season. However, this behavior has undoubtedly been exacerbated by a reduction in the vacation time available in modern employment, which is necessary for spending long periods on the islands. Harvesters therefore tend to concentrate their limited time available for harvesting on the most profitable periods of the season. Based on our data, and providing harvesting behavior remains similar, restricting harvesting to just the Rama period may reduce harvest by about 20%.

Secondly, harvesting rate, and thus harvest per day, decreased linearly with a reduction in chick density, measured before the harvesting season commenced. The role of these negative feedback mechanisms in determining harvest impacts can only be assessed through integration of data on human harvesting behavior and sooty shearwater demography.

MANAGEMENT IMPLICATIONS

Our models demonstrated that harvester effort was the predominant factor influencing sooty shearwater harvests in southern New Zealand. As the population of Rakiura Māori with hereditary rights to harvesting grows, the density of harvesters may also increase. Increased regulation of various aspects of harvester behavior such as length of the harvesting season may be an important management option for sustaining future harvests and conserving sooty shearwater populations. Based on our estimates of time worked per day (harvesting and processing) it appears that most harvesters would not have the ability to compensate for reduced season length by increasing daily harvest. Furthermore, the relationship that we observed between harvest intensity and area of manu per person provides a simple means for managers to achieve desirable levels of harvest intensity by manipulating densities of harvesters.

Further research that integrates our results, harvester behavior, and harvesting scenarios, coupled with shearwater demography, will be needed to determine the sustainable levels of shearwater harvest intensity. Decision makers (i.e., the harvest community) will then be able to compare strategies that accomplish these target intensities and select those that are socially and economically desirable.

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