Evidence-based culling of a facultative predator: Efficacy and efficiency components

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\textbf{ABSTRACT}

Human activities have greatly modified predator–prey dynamics within seabird communities by favouring a rapid increase in density of large predatory gulls. To counteract such a subsidized growth, conservation agencies perform massive random culling programs, which generally fail to restore the original predator–prey relationship. We used long-term individual-based information to evaluate the effects of a selective culling of a top seabird predator, the yellow-legged gull (\textit{Larus michahellis}), on the predatory pressure, survival and reproductive success probabilities of a secondary prey, the vulnerable European storm-petrel (\textit{Hydrobates pelagicus}). The selective removal of only 16 gulls in 3 years led to a reduction of ca. 65\% in the number of petrels killed, and to a relative increase in their survival and breeding success probabilities of 16\% and 23\%, respectively. Our results show that only a few specialised predators were responsible for the bulk of the impact on a secondary prey and that the removal of those specialised individuals was an effective and efficient way to improve prey demographic parameters.

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1. Introduction

Seabird communities are characterized by networks of multiple interactions among species; many of these have been much altered in recent times by human induced changes in marine resources (Stenhouse and Montevecchi, 1999; Solé and Montoya, 2001; Votier et al., 2004b). These alterations have modified predator–prey dynamics within seabird communities owing to the negative effects of fisheries on fish stocks and by the increase of alternative food supplies, such as urban tips and fishery discards, which subsidize predators (Votier et al., 2004b; Furness et al., 2007). Gulls are the classic example of species affected by these deep and rapid changes; over the last century their populations have increased substantially (Oro et al., 1995; Thibault et al., 1996; Duhem et al., 2008) up to the point that large gulls are currently perceived as a pest by wildlife managers, for a large number of reasons, including their impact on smaller and threatened syntopic species (Feare, 1991; Vidal et al., 1998; Finney et al., 2003; though see Oro and Martínez-Abraín, 2007). As a consequence, many conservation agencies have set up culling programs to control gull populations, which typically consist of systematic removal of large numbers of eggs, chicks or breeding adults (e.g. Blokpoel and Spaans, 1991). These programs are generally conducted at the local population level assuming that all individuals equally contribute to, or are equally responsible for, the conservation problem identified. This assumption is rarely supported...
and in most cases the systematic culling ends up being inefficient and unjustified (Oro and Martínez-Abraín, 2007). On the contrary, Brooks and Lebreton (2001) showed that the optimal harvest strategy to limit the number of yellow-legged gull (Larus michahellis) breeding pairs is to cull those individuals with the highest site/state-specific reproductive values. Likewise, the impact of predators may be only due to a few individuals specialised on a particular food item. Individual specialisation in diet is well documented in many animal taxa such as fish (e.g. Svanback and Persson, 2004), mammals (e.g. Estes et al., 2003) and birds (e.g. Spear, 1993; Hario, 1994; Guillemette and Brousseau, 2001; Martínez-Abraín et al., 2003; Oro et al., 2005). In these cases, the optimal harvesting strategy would be to eliminate only specific individuals, regardless of their reproductive value, since a small number of specialist individuals may account for a significant proportion of particular prey consumed (Votier et al., 2004c). If effective, this strategy would minimize the cost of the control program and the impact of the predator leaving its total numbers almost untouched.

The most common facultative predator of seabird species in the Mediterranean basin is the yellow-legged gull (Larus michahellis) breeding pairs is to cull those individuals with the highest site/state-specific reproductive values. Likewise, the impact of predators may be only due to a few individuals specialised on a particular food item. Individual specialisation in diet is well documented in many animal taxa such as fish (e.g. Svanback and Persson, 2004), mammals (e.g. Estes et al., 2003) and birds (e.g. Spear, 1993; Hario, 1994; Guillemette and Brousseau, 2001; Martínez-Abraín et al., 2003; Oro et al., 2005). In these cases, the optimal harvesting strategy would be to eliminate only specific individuals, regardless of their reproductive value, since a small number of specialist individuals may account for a significant proportion of particular prey consumed (Votier et al., 2004c). If effective, this strategy would minimize the cost of the control program and the impact of the predator leaving its total numbers almost untouched.

The yellow-legged gull is a large long-lived gull (average body mass, 800–1500 g, Cramp and Simmons, 1977). Eggs, usually three, are laid from mid March to early May and incubated for 27–31 days and the young birds fledge after 35–40 days. Nests are typically built on the ground or on cliff ledges. Gull territories are defended by both sexes and in stable habitats, e.g. rocky islands as opposed to sandy islands, gulls often show a high degree of fidelity to colony sites (Mac Nicholl, 1975; Burger and Lesser, 1980). An average of 535 pairs of yellow-legged gulls (median = 515, range = 300–750) have bred annually at Benidorm during the last 10 years, with a mean population growth rate of 6% during 1993–2007 (95%CI = 1.04–1.09) (see also Oro and Martínez-Abraín, 2007). Gulls nest mostly on open ground but a few pairs breed in close proximity to the two major petrel colonies.

The European storm-petrels are small (average body mass, 28 g, Warham, 1990) and long-lived vulnerable seabirds. They are single egg layers with an extended breeding period (incubation lasts about 40 days and chick rearing about 63–70 days). Earliest clutches are laid in the second half of April and the last eggs are laid in the first week of July (Mínguez, 1994). Most fledglings leave colonies in August (Mínguez, 1994). At their breeding colonies, adult European storm-petrels return to land only during the hours of darkness (Mínguez, 1996). Despite the prevalence of nocturnal activity, petrel eyes show no obvious adaptations for life in the night (Warham, 1988). In fact, storm-petrels use odour signals to find their nest (De León et al., 2003). It is likely that adult storm-petrels are captured by gulls at night when they land before entering the protection of their nesting sites. In addition, gulls can take young petrels, which venture to the entrance of their burrows to exercise their wings (Sultana and Gauci, 1970). The breeding population of storm-petrels at Benidorm island has been estimated at more than 400 pairs (Mínguez, 1994). Petrels breed all around the island at low densities but concentrate at high densities in two natural caves, where more than 300 pairs breed. We focused on data from the largest breeding colony (>200 breeding pairs), where most predation events were recorded (Oro et al., 2005). Since 1993 breeding storm-petrels were captured and marked in their nests with stainless steel bands, with a unique alphanumeric code. Breeding birds were captured only once during the breeding season to minimize disturbance, but nests were inspected at least four times during the whole breeding period to record breeding success (Mínguez, 1994; Tavecchia et al., 2008).

2. Methods

2.1. Study area and predatory–prey dynamics

The study was conducted from 1993 to 2007 at Benidorm Island (6.5 ha; 38°30′N, 0°08′E), a Special Protection Area for the conservation of the European storm-petrel species in the western Mediterranean coast of Spain. Gull numbers on the island have recently increased and evidence of predation on storm-petrels (see below) has encouraged managers to control the yellow-legged gull population.

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2.2. Evidence of gull predation and design of the selective culling

Evidence of petrel predation by gulls on the study site has been known for a long time but only since the gull population increased have there been attempts to quantify its impact (Diez and Martínez-Abraín, 1989; Massa and Sultana, 1993; Mínguez, 1994). Petrel predation was assessed by the inspection of indigestible food items in pellets collected opportunistically near gull nests or around the petrel colony during 1993–2001. Although the whole island is inspected by researchers and wardens regularly for different monitoring tasks, fewer than 10 pellets containing petrel remains per year were found far from petrel colonies. From 2002 to 2007, we standardized pellet collection with a systematic search at the vicinity of petrel colonies (see details in Oro et al., 2005). The minimum number of petrels killed by gulls was estimated as half the number of pellets containing petrel remains found because gulls produce two pellets for every storm-petrel eaten (Oro et al., 2005). We identified those pairs that predated upon storm-petrels by searching for pellets from April to June within three meters around gull nests, an area that we arbitrary identified as a gull territory (Oro et al., 2005). About 50 territories of gulls were inspected annually for evidence of predation to identify ‘specialist’ pairs, i.e. with more than one pellet with petrel remains found in their territories (Oro et al., 2005). The impact on marked birds was quantified by the number of rings of breeding petrels recovered in gull pellets. The impact of gull predation before and after the culling program was compared using a \( R^2 \) test.

The Environmental Monitoring Service of Benidorm Island (Natural Park Serra Gelada-Generalitat Valenciana) and personnel from the Endangered Species Research Team (Generalitat Valenciana) carried out an egg-pricking program from 2001 to 2006 with no apparent effects on gull numbers (Martínez-Abraín et al., 2004) or on the number of pellets containing petrels’ remains (this study). A second measure of control was to selectively remove those gulls that bred near petrel colonies thought to be responsible for most predation events (Borg et al., 1995; Adam and Booth, 2001; Oro et al., 2005). From 2004 to 2005 a total of six gulls breeding in territories previously identified as belonging to ‘specialist’ pairs (i.e. one pair that bred inside the petrel’s cave and two individuals belonging to two different territories located outside the cave in 2004, plus two individuals that bred in two territories located outside the cave in 2005) were captured with nest traps placed on the nests. In 2006, 10 additional individuals (i.e. three pairs plus four individuals from different territories) were trapped on nests located at the edge of the petrel colony as a precautionary measure. In all cases nests were deserted. All individuals were killed by an authorised wildlife agent through the injection of an excess sedative in the jugular vein.

2.3. Demographic parameters and culling efficacy

Adult survival probability of petrels was estimated from 1858 observations of 675 breeding adults marked from 1993 to 2007. These data were analyzed using capture-recapture models, which estimate survival and detection probabilities simultaneously (see details in Lebreton et al., 1992; Amstrup et al., 2005). The analysis compared models in which survival and recapture probabilities depended on a different combination of the factors considered (see below). Models were selected using Akaike’s Information Criterion (AIC) and Akaike weights \( w_1 \), for each model \( j \) were calculated as an index of the strength of evidence of each model (Burnham and Anderson, 2002). Model selection began by assessing the goodness of fit of a general model in which all parameters were time-dependent, i.e. the Cormack–Jolly–Seber model (Lebreton et al., 1992), by contingency tables, together with the Chi-square statistic, using program U.CARE 2.2.2 (Choquet et al., 2005). Model deviances and AIC values were calculated using program M-SURGE (Choquet et al., 2004).

Average breeding success was modelled as a binary variable (1 = successful, 0 = unsuccessful) using generalized linear mixed models with a logit-link function and binomial error distribution (McCulloch and Searle, 2001). Analyses were conducted with the R statistical package (http://www.R-project.org/) using the glmmML function in which ‘year’ (15 levels) was considered a fixed term and the nest identity treated as a random term to prevent pseudoreplication.

Together with identifying the most parsimonious model to describe the parameter considered, our analysis also aimed to test for a difference in survival and breeding success before and after the selective culling. The comparison was done using a likelihood ratio test (LRT, Lebreton et al., 1992) between a model including a single parameter for 1993–2007 with one assuming two parameters, one for the period before the culling (1993–2003) and a second for the period after (2004–2007, denoted ‘culling’ in model notation). The test was based on the change of deviance between the two nested models.

3. Results

3.1. Evidence of gull predation and selective culling

The number of pellets containing petrel remains found during April and May 2004, when the selective culling began, was similar to the one in previous years. However, after the removal in early June of a single gull the evidence of predation decreased drastically (see Fig. 1). This last individual was the male from a pair breeding inside the cave where the petrel colony is located, so their breeding territory was within the petrel colony. In 2005 and 2006 the number of pellets containing petrel remains remained low with the exception of August 2006, when a group of juvenile gulls spent several nights inside the cave that hosts the colony (direct observation, Fig. 1). A few of the gull territories from which adult gulls were removed were recolonized during 2007 when culling was stopped. There was no apparent increase in predation rates following this colonisation (Fig. 1). Overall, removal of only six specialised gull and 10 additional individuals nesting in the proximity of the cave led to a mean reduction of 65% (95%CI = 57–72) in the number of petrels found in gull pellets (\( \chi^2 = 157.14, \text{d.f.} = 1, P < 0.001 \)) (Table 1, and Fig. 1). After 2004 we also found a mean reduction of 89% (95%CI = 85–94) in the number of metal rings of breeding petrels inside the pellets compared with the period 2002–2003 (\( \chi^2 = 18.38, \text{d.f.} = 1, \))
The overall test of goodness of fit of the CJS model was statistically significant ($\chi^2 = 96.18$, d.f. = 46, $P < 0.001$) because newly marked birds had a lower survival than birds already marked ($\chi^2 = 48.12$, d.f. = 13, $P < 0.001$), and the current recapture probability depended on the past recapture probability ($\chi^2 = 27.91$, d.f. = 12, $P = 0.006$). As a consequence we considered a model with two age-classes for survival parameters (a model including a ‘transient’ effect as detailed in Pradel et al., 1997) and we used a variance inflator factor, $\delta$-hat, calculated as the ratio of the global chi-square statistic on its degrees of freedom, to correct for the residual lack of fit ($\delta$-hat = 1.46; Lebreton et al., 1992). In agreement with a previous study (Tavecchia et al., in press) specialist adult gulls can be individually identified.
and removed at the beginning of the petrel breeding period due to their territorial habits (i.e. remains of their main prey can be easily found around their nests). Unfortunately, culling of territorial specialist gulls cannot alleviate predation by juveniles. Presence of juvenile gulls inside caves where petrels breed is common from July to September (Mínguez and Oro, 2003). Nevertheless, at Benidorm Island predation by juvenile gulls seems to have a strong stochastic component. For example, predation by juvenile gulls was recorded in 2006 but not in 2004, 2005 or 2007. Identification of specialist juveniles is nearly impossible even by direct observation of predation events. Despite this, it is likely that juvenile gulls prey upon fledgling petrels rather than adults, so have a much reduced impact on petrels’ population growth rate (Saether and Bakke, 2000). The success of the management actions implemented at Benidorm Island encourages management decision-making based on previous evidence. Studies investigating the effectiveness of interventions are highly relevant to practitioners but few studies actively test or review conservation actions (Fazey et al., 2005; Armstrong and Seddon, 2008).

During the last year of study no gulls were removed and predation rates continued at low levels, suggesting that most

<table>
<thead>
<tr>
<th>Model</th>
<th>p</th>
<th>(\phi_{\text{transients}})</th>
<th>(\phi_{\text{residents}})</th>
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<th>dev</th>
<th>QAIC</th>
<th>(\Delta_i)</th>
<th>(w_i)</th>
</tr>
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<tbody>
<tr>
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<td>.</td>
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<tr>
<td>3</td>
<td>t</td>
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<td>t+</td>
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<td>2790.99</td>
<td>2098.51</td>
<td>0</td>
<td>0.83</td>
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<td>26.85</td>
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<td>.</td>
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<td>2112.23</td>
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<td>.</td>
<td>t</td>
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<tr>
<td>7</td>
<td>t</td>
<td>t</td>
<td>cull</td>
<td>30</td>
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<td>2101.87</td>
<td>3.36</td>
<td>0.16</td>
</tr>
<tr>
<td>8</td>
<td>t</td>
<td>cull</td>
<td>cull</td>
<td>18</td>
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<td>12.73</td>
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<td>2118.77</td>
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<td>2125.94</td>
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specialist gulls were removed in previous years. Although gulls from reoccupied territories inside the cave holding the petrel colony did not specialise as petrel predators in 2007, monitoring and management actions should be implemented on an annual basis, since gulls can readily occupy such a foraging niche (Spear, 1993; Guillemette and Brousseau, 2001). Moreover, new fishing and environmental policies, including reductions of trawling discards and closure of landfills, will reduce important foraging resources for gull populations (Oro et al., 2006). Under this scenario it is expected that facultative predators increase predation rates on smaller syntopic species (Stenhouse and Montevecchi, 1999; Votier et al., 2004b). Intensive control measures are often very onerous (Table 4) and necessitate heavy manpower and resources. Egg-pricking is an efficient method to reduce gull nesting success (Smith and Carlile, 1993), nevertheless adults remain alive at colonies and may continue preying upon vulnerable species. Culling of breeding adults can be carried out by placing poisoned baits in gull nests (Bosch et al., 2000) or with nest traps (this study). The first technique requires one visit to place the first bait in each nest, a new visit to remove the dead gulls and to place new baits, and a final visit to remove both newly killed gulls and any remaining bait (Bosch et al., 2000). Several hours are allowed to elapse between consecutive visits, allowing narcosis. Moreover, it is necessary to transport culled birds to land in order to remove them by incineration and search those that died at sea from a boat to prevent secondary poisoning (Bosch et al., 2000). Placing nest traps to capture gulls is much more time consuming than placing poisoned baits and it would be impractical for a massive culling program (Table 4). Massive culling programs can be successful to reduce gull numbers or reduce the effect of gull predation (Bosch et al., 2000; Finney et al., 2003; Paracuellos et al., 2006) only at small temporal and spatial scales (Skira and Wapstra, 1990; Bosch, 1996; Harris and Wanless, 1997; Vidal et al., 1998; Oro and Martínez-Abrain, 2007). In addition, massive random culling programs have the indirect effect of enhancing dispersal (Coulson, 1991; Bosch et al., 2000), so that the reduction in gull numbers in a local population may be rapidly compensated by an increase of recruitment due to density-dependent regulation (Brooks and Lebreton, 2001). Moreover, culling on adult birds has the potential to increase young survival because of decreased competition for food resources that remain at a static level (Coulson et al., 1982). Thus, to substantially reduce gull numbers at a metapopulation level it may be necessary to kill a large number of individuals for a long period, which is an expensive and polemic solution (Bosch et al., 2000).

The implementation of specific culling programs is both time and resource consuming but such costs are negligible compared to the traditional solution of a systematic massive culling of individuals, not to mention social or ethical costs (Oro and Martínez-Abrain, 2007) as well as unforeseen and unwanted side effects (Martínez-Abrain et al., 2004). This is especially true when most predation is caused by specialist gulls, and consequently massive random gull culling may not be a practical solution (Hario, 1994). A massive culling program performed in Alborán Island, Western Mediterranean, Spain, from 2000 to 2006, successfully removed around 28.6% (range: 16–45%) of pairs breeding in the island annually (Mariano Paracuellos, com. pers.). Similar results were obtained through a systematic massive culling at Medes Islands, where between 21% and 29% of the breeding adults were killed annually (Bosch et al., 2000). Consequently, the presence of specialist predators may be omitted from a general cull just by chance. Specialist bird predators defend breeding

<table>
<thead>
<tr>
<th>Model</th>
<th>Effects</th>
<th>K</th>
<th>dev</th>
<th>AIC</th>
<th>ΔAIC</th>
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</tr>
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<td>3</td>
<td>.</td>
<td>1</td>
<td>2694</td>
<td>2698</td>
<td>79</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 3 – Breeding success of European storm-petrels analyzed through Generalized Linear mixed modelling; K: number of parameters; dev: relative deviance; AIC: Akaike information criterion; ΔAIC: the AIC difference between the current and lowest AIC model; wi: Akaike’s weight. Model notation: ‘t’ = yearly variation, ‘cull’ = effect of culling (two parameters for the period 1993–2001 and 2002–2007, respectively), ‘.’ = constant (i.e. no effects considered). The model retained is in bold.

<table>
<thead>
<tr>
<th>Costs (h)</th>
<th>Nest traps</th>
<th>Poisoned baits</th>
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<tr>
<td></td>
<td>Specific</td>
<td>Massive</td>
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<tr>
<td>Preparing baits</td>
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<td>0</td>
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<tr>
<td>Search ‘objective’ nests</td>
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<tr>
<td>Setting traps or baits</td>
<td>2.5</td>
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</tr>
<tr>
<td>Kill gulls</td>
<td>1.66</td>
<td>133</td>
</tr>
<tr>
<td>Recollect dead gulls</td>
<td>1.66</td>
<td>133</td>
</tr>
<tr>
<td>Total</td>
<td>30</td>
<td>467</td>
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Table 4 – Estimates of time costs (hours) for specific (10 individuals) and massive (800 individuals) gull culling programs using nest traps to capture gulls or by narcotizing gulls whit poisoned baits. We considered 100% of effectiveness (i.e. both members of the pair die). We considered for each strategy: Preparing baits = 2 min/bait; Setting traps = 15 min/trap; Setting baits = 3 min/bail; Kill gulls = 10 min/gull; Recollect dead gulls = 10 min/gull. Note that for the sake of simplicity costs for people, for transport of dead gulls or for the search of nests or gulls dead at sea were not considered.
and feeding territories, retain their feeding habit and feeding territory across years (Votier et al., 2004a). Removing only specialised individuals is a much more efficient solution to protect species of conservation-concern when threatened by excessive predation owing to human subsidizing of predators (e.g. increased predator density by increased availability of food resources) (Shapira et al., 2008; Gompper and Vanak, 2008). Our study clearly illustrates the great potential of evidence-based wildlife management (Pullin et al., 2004) in terms of resource optimization and successful achievement of desired conservation goals.

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