Bird Conservation International (2007) 17:63–77. © BirdLife International 2007
doi: 10.1017/S0959270906000621 Printed in the United Kingdom

Vulture restaurants and their role in reducing diclofenac exposure in Asian vultures

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Summary

The provision of supplementary food at vulture restaurants is a well-established tool in the conservation of vulture species. Among their many applications, vulture restaurants are used to provide a safe food source in areas where carcasses are commonly baited with poisons. Rapid and extensive declines of vultures in the Indian subcontinent have been attributed to the toxic effects of diclofenac, a pharmaceutical used in the treatment of livestock, to which vultures are exposed while feeding on the carcasses of treated animals. A vulture restaurant was established at the Oriental White-backed Vulture *Gyps bengalensis* colony at Toawala, in Punjab province Pakistan, to test the effectiveness of the technique in modifying ranging behaviour and mortality at the colony. Six male vultures were fitted with satellite transmitters to describe variation in movement and home-range during periods when safe food was alternately available and withheld at the vulture restaurant. There was considerable variation in individual home-range size (minimum convex polygons, MCP, of 1,824 km^2 to 68,930 km^2), with birds occupying smaller home-ranges centred closer to the restaurant being more successful in locating the reliable source of food. Fixes showed that 3 of the tagged vultures fed at the vulture restaurant and the home-range of each bird declined following their initial visit, with a 23–59% reduction in MCP. Mean daily mortality during provisioning was 0.072 birds per day (8 birds in 111 days), compared with 0.387 birds per day (41 birds in 106 days) during non-provisioning control periods. Vultures tended to occupy greater home-ranges, cover greater distances each day and spend proportionately more time in the air during the late brooding and post-breeding seasons. Attendance at the vulture restaurant also declined during this period with fewer birds visiting less often and no tagged vultures visiting the vulture restaurant at all. These findings indicate that vulture restaurants can reduce, but not eliminate, vulture mortality through diclofenac exposure and represent a valuable interim measure in slowing vulture population decline locally until diclofenac can be withdrawn from veterinary use.

Introduction

The populations of three species of *Gyps* vulture in the Indian subcontinent have undergone rapid and extensive declines since the early 1990s (Prakash 1999, Gilbert *et al.* 2002, Prakash *et al.* 2003). As a result, the Oriental White-backed Vulture *Gyps bengalensis*, Long-billed Vulture *G. indicus* and Slender-billed Vulture *G. tenuirostris* have been classified as Critically Endangered (IUCN 2004). Population declines have been associated with high rates of mortality affecting all age classes (Prakash 1999, Gilbert *et al.* 2002), with annual mortality estimated between 22% and 50% (Green *et al.* 2004). Examinations of large numbers of dead vultures in Pakistan found that acute renal failure, manifested as visceral gout, was the proximate cause of death in 85% of adult and sub-adult birds and renal failure was due, ultimately, to the toxic effects of diclofenac (Oaks *et al.* 2004). Diclofenac is a pharmaceutical used regionally to treat inflammation and fever in livestock. Residues of diclofenac were found in all ($n = 25$) field cases of visceral gout tested, whereas vultures dying from other causes were all negative for the drug ($n = 13$). Subsequently, tissues collected from 14 vultures with visceral gout in India and Nepal between 2000 and 2004 were also shown to contain diclofenac residues (Shultz *et al.* 2004) and a simulation model has demonstrated that diclofenac is at least the primary, and possibly only cause of the vulture decline across the region (Green *et al.* 2004). Removing diclofenac from the veterinary market in at least three countries will take time and, given the continued rapid population decline, any measures that can reduce diclofenac exposure in the interim will be of considerable benefit to *Gyps* vultures.

The provision of supplemental food at 'vulture restaurants' is well established as a management tool in the conservation of vulture populations (Mundy *et al.* 1992). In its simplest form carcasses are provided in areas with insufficient food (Wilbur *et al.* 1974, Meretsky and Mannan 1999) or where nutrient availability is considered inadequate (Richardson *et al.* 1986). Supplementary feeding was shown to increase the survival of first year Cape Vultures *Gyps coprotheres* at Potberg in South Africa (Piper *et al.* 1999), has been employed during successful reintroduction programmes (Sarrazin *et al.* 1994, Terrasse *et al.* 1994), and has facilitated the recolonization of abandoned breeding sites (Mundy *et al.* 1992). Vulture restaurants have been used to provide alternative sources of uncontaminated food in areas where carcasses are baited with poison to control carnivore populations (Wilbur *et al.* 1974, Terrasse 1985, Johnson *et al.* 1998, Susic and Pavokovic 2003). However, the effectiveness of this approach remains largely untested, particularly in areas where food availability is high such as Pakistan's Punjab province.

This study aims to determine whether vulture restaurants are effective in reducing vulture exposure to diclofenac and subsequent mortality. The study measures mortality at a colony during breeding and non-breeding periods when supplementary food was alternately available and withheld. Platform terminal transmitters (PTTs) were used to record the movement of vultures with global positioning system (GPS) accuracy to determine whether food provisioning is able to modify home-range and foraging behaviour.

Methods and materials

Study area

Punjab province is dominated by the Indus basin, a broad, flat alluvial floodplain formed by the five major tributaries of the Indus River and ranges from 82 to 276 m in elevation (Figure 1). Human and livestock densities are generally high with the fertile plains heavily cultivated with cotton, wheat, and mango orchards (Roberts 1991). The Thal Desert, bounded by the Indus, Chenab and Jhelum Rivers, is more sparsely populated and is dominated by tropical thorn forest and sand dunes (Roberts 1991). Mean winter temperatures can fall as low as 5.6°C in January and rise to 42.3°C in June (Pakistan Meteorological Department, Lahore, unpubl.). Annual rainfall is mainly concentrated during the monsoon months (July–September).

The vulture colony studied at Toawala (30.50550° N, 71.68662° E) lies north-east of Multan and runs along the Shujabad Canal, roughly parallel to the Chenab River. Vultures nest in trees that are unevenly distributed along a 42.5 km stretch of canal, with the majority of nests concentrated along 18.7 km at the eastern limit of the colony. The colony is occupied throughout the year, with highest numbers present during the breeding period from October to May. The majority of eggs are laid in November, with hatching in late December and early January. Juvenile vultures fledge between mid-March and May.

Vulture mortality

From 1 to 26 November 2003 the vulture colony was surveyed for dead vultures along all or part of its length on 11 occasions. Daily surveys were conducted along the entire 42.5 km of colony

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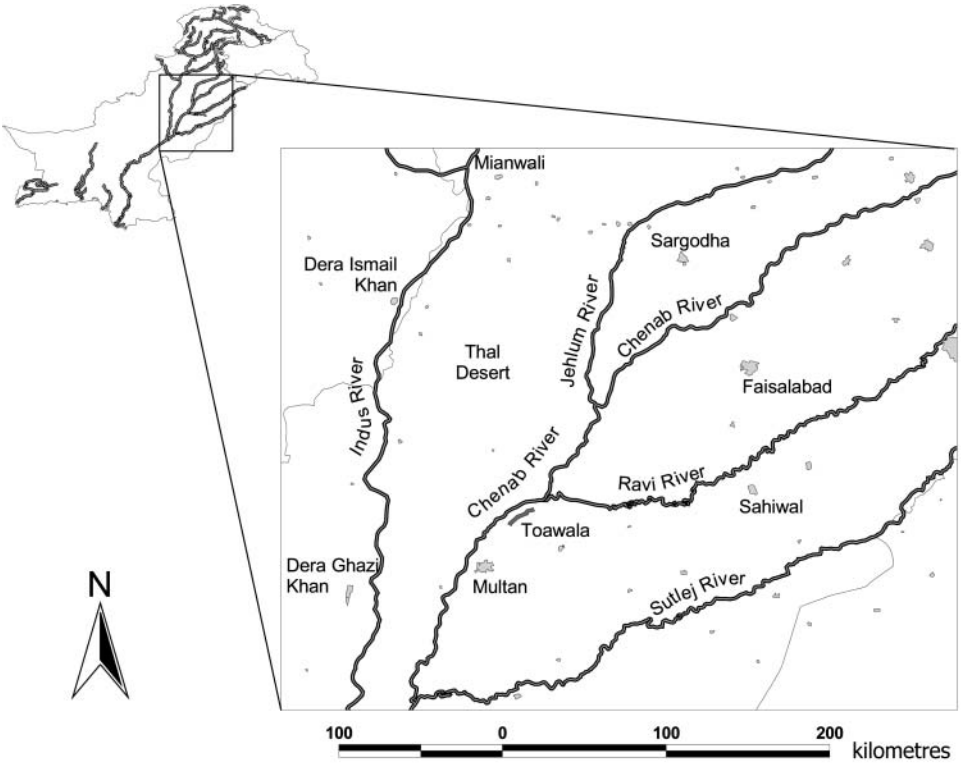

Figure 1. Map of the Punjab province, Pakistan and study area.

between 27 November 2003 and 30 June 2004. All vulture carcasses located were counted and then removed or marked to prevent double-counting. Cause of death was determined by necropsy examination on the majority of carcasses using the protocols outlined in Gilbert *et al.* (2002). It was not possible to conduct necropsies on every dead bird, as some became tangled in dead branches and could not be immediately recovered, and others were partially consumed by feral dogs soon after death.

Vulture counts

Counts of vultures roosting in the colony were made at 24 to 86 day intervals from 28 August 2003 to 22 June 2004 to measure colony size. All vultures observed along the 42.5 km colony were counted (excluding nestlings). It was not practical to traverse the whole study area in a single evening so vultures in the 18.7 km where nest density was greatest were counted within 2 hours of sunset and remaining birds counted within 2 hours of sunrise the following day.

Food provisioning

A supplementary feeding site (vulture restaurant) was established close to the densest area of the Toawala colony (30.50802° N, 71.72487° E), 3.8 km from the harmonic mean centre (the point where the inverse reciprocal mean distance to all active nests is a minimum) and 1.4 km from the closest active nest. The site consisted of an open rectangular field (67 m × 45 m) that was visible

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from the nearest nesting trees and with no overhead wires or similar aerial obstacles for at least 500 m. A 1 m high perimeter fence was erected around the field to exclude dogs and was reinforced with *Acacia* spp. branches. There were few trees in the immediate vicinity of the vulture restaurant, so four perches were erected to discourage birds from perching on nearby farm houses. A concrete pool was built during early April to provide a reliable supply of water during the hot and dry summer months. All feed animals were locally purchased donkeys and these were marked and held for a period of at least 1 week to ensure that any residues of diclofenac administered prior to purchase were eliminated from their tissues before slaughter. Although no published studies have described the pharmacokinetics of diclofenac in equines, work in humans has shown that 90% of diclofenac administered at therapeutic doses is eliminated by 96 hours (Reiss *et al.* 1978 cited in Todd and Sorkin 1988).

The study was divided into four periods. Period A (27 November to 31 December 2003) and period C (9 February to 18 April 2004) were control periods when no food was offered. Carcasses were provided to meet consumption during period B (1 January to 8 February 2004) and period D (19 April to 30 June 2004). Thus provisioning occurred during the first month of chick rearing, and during the fledging and post-fledging period. Carcasses were placed in the centre of the feeding area within 1 hour of sunrise and the upper half of the carcass was skinned to facilitate access to soft tissues. Additional carcasses were provided throughout the day depending on consumption to enable all birds to feed until satiated. Carcasses that remained untouched after 1 day quickly became dry and unpalatable so remaining skin was removed to expose fresh tissues. Fresh carcasses were provided at least every second day to ensure that there was a constant supply of freshly exposed meat at all times. Carcasses were weighed prior to being placed in the feeding area and the mass of all bones, hide and tissues removed at the end of each day were subtracted to approximate the mass of tissue consumed. Long bones were crushed and scattered around the provisioning area.

Vulture movement from GPS-PTT tracking

During November 2003, six Oriental White-backed Vultures were trapped while feeding at carcasses < 1 km from the colony using an adapted version of the padded jaw trap (Day *et al.* 1980). Each vulture was fitted with a Microwave Telemetry, Inc. solar powered GPS-PTT unit weighing 73 g (1.2–1.9% body mass). Transmitters were mounted on the patagium using the method described by Wallace *et al.* (1994) and incorporated a coloured vinyl patagial tag to aid in individual identification in the field. Hereafter these birds are identified as Black, Blue, White, Orange, Green and Yellow. The GPS-PTT units were programmed to record 13 GPS fixes at hourly intervals from 06h00 to 18h00 (local time), and download these data via satellite link every 24 hours.

All six vultures were in adult plumage when trapped and all birds were later determined to be male using molecular methods described by Ito *et al.* (2003). Their breeding status was assessed through observation of marked birds encountered opportunistically and by searching areas where vultures returned most frequently.

Data analysis

Vulture positions determined from GPS-PTT fixes were analysed using Ranges6 software v1.2 to characterize the movement and space use of individual vultures during provisioning and control periods (Kenward *et al.* 2003). A measure of daily movement distance was calculated for all days during which 10 or more fixes were obtained by summing the distances between successive fixes. Home-range area was calculated using minimum convex polygons (MCPs) that calculate the smallest polygon with external angles greater than 180° to include all fix locations (Kenward 2001). Tracking resolution was set at 20 m to take account of GPS tracking unit accuracy. Estimates of home-range using MCP methods are very sensitive to outlier positions recorded during infrequent movements outside the 'normal' area of activity (Kernohan *et al.* 2001). Such outlier positions have a disproportionate influence on MCP area; an effect that increases with time and complicates comparisons of MCP estimates made during periods of unequal duration. To counter this, outlier positions were excluded using a peeled polygon core method excluding 0, 5% and 10% of positions furthest from the harmonic mean centre (the point where inverse reciprocal mean distance to all the other fixes is a minimum) to obtain 100%, 95% and 90% peeled polygon cores. Autocorrelation or independence of fixes is an important consideration when calculating home-range using conventional radio-telemetry (Kenward 2001). However, this is not considered to be a problem in the use of GPS-PTT units so long as positions are recorded at regular intervals during the animal's normal activity cycle, thus ensuring unbiased temporal coverage of the animal's movements during the study period (Otis and White 1999).

Fixes and sensor readings obtained from the PTT units were used to determine the activity, location and, as far as possible, behaviour of tagged vultures. Positions recorded at 06h00 where vultures were immobile (speed sensor reading of 0 km/h) were considered to indicate vultures perched at roost sites. All recorded roost positions in Toawala colony were within 6 km of the vulture restaurant; thus this distance was used as an arbitrary cut-off differentiating fixes 'close to' (< 6 km) and 'distant from' (> 6 km) the restaurant.

Speed fixes greater than 10 km/h were a reliable indication that a vulture was in flight (although soaring vultures were occasionally recorded at 0 km/h, presumably indicating a bird flying into a headwind or manoeuvring in a tight circle). Roost positions did not exceed 256 m elevation above sea level for any vulture during the study period, and this was assumed to be the maximum altitude at which a vulture could be perched in the study area. Vultures were considered to be flying for all fixes obtained at altitudes exceeding 256 m, or when speed was greater than 10 km/h at altitudes less than 256 m.

Results

Food consumption and numbers of vultures at the vulture restaurant

While no birds visited the vulture restaurant during periods A or C, vultures visited the restaurant on 28 (73.7%) of 38 days when clean food was provided during period B, a time when vultures were feeding young nestlings. On the first day a single vulture landed within the fenced area but by the third day birds began arriving in significant numbers. It was not possible to determine the number of birds feeding each day; however, daily maximum counts regularly exceeded 100–200 birds with a highest count of 337 vultures on the ground on 15 January.

Substantial quantities of tissue were consumed during period B, requiring considerable effort to procure feed animals to keep pace with demand. A total of 111 carcasses (about 6,499 kg live weight) were offered of which 86 were weighed both before and after vultures had fed. Combined mass of these 86 carcasses was 5,035 kg from which 1,515 kg (30%) of hide, bones and unconsumed tissue were recovered, indicating that vultures consumed about 4,549 kg of the 111 carcasses offered. However, an additional 18 naturally available livestock carcasses were observed in the vicinity of the vulture colony during the feeding period, at least seven of which were attended by vultures. Therefore, the amount of provisioned food consumed at the vulture restaurant can not be assumed to have fed the entire colony exclusively throughout this period.

The vulture restaurant was stocked for 73 days during period D in the post-fledging period. Vultures fed on only 12 days (16.4% of days) and in smaller numbers than during period B with more than 10 birds recorded on only seven occasions and more than 100 birds recorded only once (156 birds on 20 April). The number of carcasses and mass of food consumed was not recorded during this period.

Vulture mortality

We collected 50 dead adult and sub-adult vultures during the study period. Visceral gout, indicative of renal failure possibly due to diclofenac poisoning (Oaks *et al.* 2004, Shultz *et al.* 2004), was found in 29 of 30 dead vultures that were available for necropsy. The single non-gout case was an emaciated sub-adult that was excluded from further analyses. During provisioning period B (38 days) four dead adult vultures were collected of which three were necropsied and found to have visceral gout. Three adults and a sub-adult vulture were located during provisioning period D (73 days) of which two were necropsied and both had gout.

Mean daily mortality during provisioning was 0.072 birds per day (8 birds in 111 days), compared with 0.387 birds per day (41 birds in 106 days) during non-provisioning control periods. Because the abundance of vultures in the colony varied dramatically between seasons, we compared mortality between provisioning and non-provisioning periods only within each season. Mortality in the non-provisioning control period A (25 birds in 35 days) was significantly higher than during provisioning period B (4 birds in 38 days, $\chi^2_1 = 17.1$, $P < 0.001$). Likewise, mortality in the non-provisioning control period C (16 birds in 71 days) was significantly higher than during provisioning period D (4 birds in 73 days, $\chi^2_1 = 7.5$, $P = 0.006$).

Vulture counts

Numbers of adult and sub-adult vultures roosting at the colony varied through the breeding season, reaching a maximum count of 537 on 26 December 2003 when eggs were beginning to hatch, and declining thereafter to reach a low of 280 on 16 May 2004 after all the nestlings had fledged (Figure 2).

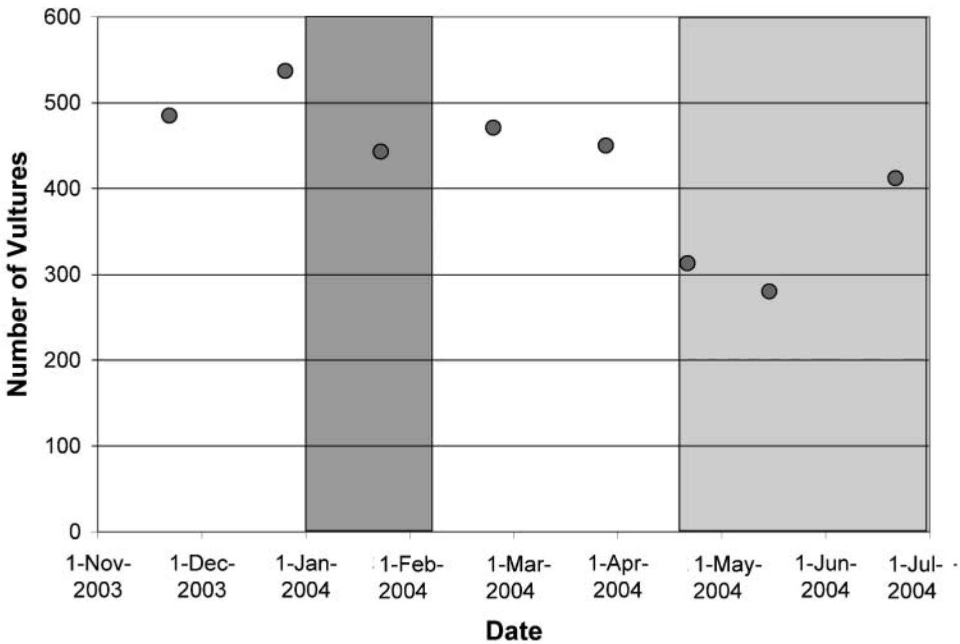

Figure 2. Combined counts of roosting adult and sub-adult vultures at Toawala colony between 28 August 2003 and 22 June 2004. Shaded areas indicate periods during which the vulture restaurant was operational.

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GPS-PTT performance

Five of the six GPS-PTT units performed very well, with a mean number of daily fixes of 11.8 for Blue (n = 230 days, SD ± 1.65), 10.6 for White (n =228 days, SD ± 3.08), 12.2 for Orange (n = 229 days, SD ± 1.96), 11.6 for Green (n = 215 days, SD ± 2.46) and 9.7 for Yellow (n = 215 days, SD ± 3.11). The units failed to obtain any GPS fixes on only 1 (Blue), 3 (Orange, Green), 8 (White) and 11 days (Yellow), corresponding to periods when cloud cover, rain or dust storms prevented the solar-powered units from charging sufficiently. Due to a hardware problem the unit attached to the Black bird did not charge effectively, and GPS locations were received for only 31 days following attachment. Because the location fixes for this bird are incomplete, its home-range and movement characteristics could not be reported.

Vulture movement and biology

The home-ranges traversed by the Yellow and Orange vultures were considerably greater than those of Blue, White and Green, with MCPs calculated across the study period of 68,930 km^2, 40,324 km^2, 4,625 km^2, 1,824 km^2 and 5,069 km^2, respectively (Figure 3). The Yellow vulture moved widely, circumnavigating the Thal Desert on nine occasions during the study period and ranging up to 257 km from Toawala. This vulture utilized multiple roost-sites across the Punjab including several known extant or recently extinct Oriental White-backed Vulture colonies, roosting within 6 km of the restaurant on only 16.8% (n = 196) nights where roost location could be established. In contrast, the Blue, White and Orange birds roosted within 6 km of the

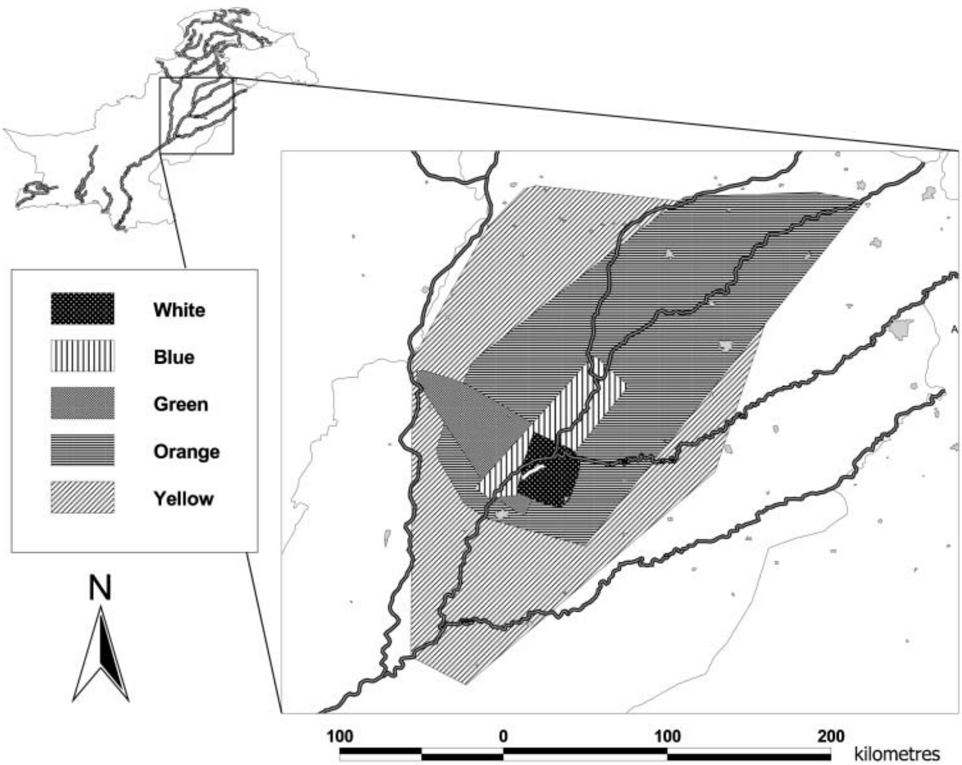

Figure 3. The home-range of satellite-tagged vultures during the study period, expressed using the minimum convex polygon (MCP) method.

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restaurant site on 79.3% (n = 228), 88.0% (n = 216) and 48.2% (n = 224) nights respectively. These birds ranged up to 102 km (Blue), 35 km (White) and 316 km (Orange) from the colony.

Only one of the tagged vultures showed breeding activity during the study period, with the Green vulture observed incubating in December in an atypically solitary nest 24 km north-west of Toawala. The movements of this bird suggest that the nest hatched in early January, but failed approximately 2 weeks later. During the 53 days prior to the failure of this nest the Green bird occupied a home-range of 3,014 km^2 and moved up to 90 km from the nest-site.

Visits to the vulture restaurant, home-range, roost-site use, mean daily distance travelled and mean daily time in flight varied between individual vultures, during control and provisioning periods, and as the breeding season progressed through the study period. The large number of independent variables potentially influencing vulture behaviour and the small number of vultures tagged makes statistical analysis difficult. However, by comparing parameters between successive control and provisioning periods, A to B, and C to D, and looking for common patterns among the individual vultures, we can describe the following behavioural effects of food provisioning on vulture ranging behaviour.

Periods A and B

During provisioning period B, fixes placed four of the six GPS-PTT birds within 6 km of the vulture restaurant, three of which made visits before provisioning ceased on 8 February. Blue and White made their first visits to the vulture restaurant on the 3 January and had visited on 11 and 20 days, respectively, by the end of the period 36 days later. Orange failed to locate the restaurant during the first 12 days of period B, roosting at a maximum distance of 74 km and passing within 6 km of the vulture restaurant on two occasions. It made its first visit to the vulture restaurant on 13 January and was subsequently recorded there on 11 of the remaining 26 days before provisioning was discontinued.

The PTT unit attached to Black ceased transmitting GPS fixes at 18h00 on 2 January, at which time this bird was roosting along a canal 16 km north of the vulture feeding site. However, the unit continued to transmit Argos positions for a further 20 days, providing a record of the bird's movements until 22 January. Eight fixes (class 2 or 3) were received from the Black-tagged bird's transmitter within 6 km of the vulture restaurant on 4 days from 19 January until it ceased working. This bird was not observed at the feeding site at any time, despite its proximity on at least these 4 days.

The attendance of tagged vultures at the restaurant is given in Table 1. Vultures are estimated to feed every 2–4 days (Green *et al.* 2004). Tagged vultures were absent for more than 4 days on two (Blue), one (White) and two (Orange) occasions, suggesting that birds may occasionally have been feeding at carcasses outside the restaurant. No tagged vultures were recorded at the restaurant after 1 February, although vultures did feed at the restaurant on 2 of the remaining 6 days during which food was available.

Food was available for 36 days following the first visit to the restaurant made by Blue and White, and 26 days for Orange. Home-range for each bird over an equivalent period prior to the location of the restaurant was used to compare MCPs when food was alternately withheld and available. The home-range of each bird declined following their discovery of the restaurant, with a 23–59% reduction in MCP of 291 to 119 km^2 (White), 395 to 306 km^2 (Blue) and 3,555 to 1,996 km^2 (Orange) (Table 2). Green and Yellow did not discover and visit the vulture restaurant at all during the 38 days of period B. Positions were available for Green and Yellow only after 29 November, so home-ranges during the 32 day period prior to and following the start of feeding were compared. Green's home-range decreased by 49% from 3,014 km^2 in period A to 1,546 km^2 in period B, while Yellow's home-range increased by 6% from 22,075 to 23,396 km^2 (Table 2).

Vultures were more likely to roost close to the vulture restaurant once they had located the predictable source of food. Prior to locating the restaurant Orange roosted within 6 km on 34

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Table 1. Attendance of satellite-tagged vultures (Blue, White and Orange) at the vulture restaurant during Period B.

	1-Jan	2-Jan	3-Jan	4-Jan	5-Jan	6-Jan	7-Jan	8-Jan	9-Jan	10-Jan	11-Jan	12-Jan	13-Jan	14-Jan	15-Jan	16-Jan	17-Jan	18-Jan	19-Jan
Blue			√					√				√			√	√		√	√
White			√			√		√		√		√		√	√	√	√	√	√
Orange													√	√	√	√	√	√	

	20-Jan	21-Jan	22-Jan	23-Jan	24-Jan	25-Jan	26-Jan	27-Jan	28-Jan	29-Jan	30-Jan	31-Jan	1-Feb	2-Feb	3-Feb	4-Feb	5-Feb	6-Feb	7-Feb
Blue	√		√			√	√												
White	√		√	√		√	√	√	√			√	√						
Orange						√	√	√			√		√						

Table 2. Vulture home-range (km^2) expressed using the minimum convex polygon (MCP) method.

	Period A	Period B	Period C	Period D	All periods
Blue	395[a]	306[b]	2,737	3,230	4,625
Orange	3,555[a]	1,996[b]	32,201	10,691	40,324
White	291[a]	119[b]	1,633	760	1,825
Green	3,014[c]	1,549[c]	1,572	1,874	5,069
Yellow	22,075[c]	23,396[c]	66,817	38,015	68,930

[a]MCP during a period equivalent to ''b'' prior to the discovery of the vulture restaurant.
[b]MCP following initial discovery of the vulture restaurant to the end of 7 February when food was withdrawn.
[c]MCP during the 32 days prior to and following the onset of feeding on 1 January.

(59%) of 58 nights where roost site was established, and Blue on 33 (66%) of 50 nights. Once vultures were aware of the reliable source of food they roosted close to the vulture restaurant more frequently, with Orange roosting within 6 km on 16 (70%) of 23 nights and Blue on 32 (91%) of 35 nights. White remained highly faithful to the vulture restaurant throughout periods A and B, roosting within 6 km on 44 (92%) of 48 nights before discovering the site and 27 (90%) of 30 nights afterwards.

Mean daily distance travelled by Blue, White and Orange declined significantly ($t = 4.19$, $P < 0.001$, d.f. = 154) once these birds located the vulture restaurant (Table 3). In contrast, mean daily distance moved by vultures not visiting the vulture restaurant (Yellow and Green) was higher during period B than A. Mean daily time in flight also decreased once birds discovered the restaurant ($t = 7.77$, d.f. = 2, $P = 0.016$), whereas it increased for Yellow and Green from period A to B (Table 3).

Vultures did not visit the vulture restaurant every day and continued to range and sometimes roost at distant locations. Orange roosted more than 6 km from the restaurant on at least seven occasions ($n = 20$, roost-site could not be determined for six) during period B and ranged up to 42.6 km. Blue and White roosted more than 6 km on three occasions ($n = 36$), and ranged up to 22.3 and 11.6 km, respectively. It was not possible to confirm whether vultures were feeding during these forays; however, it was possible to differentiate perched fixes, when vultures may have been feeding using altitude (< 256 m) and speed sensors (< 10 km/h). If perched positions within 200 m of roost locations are excluded, then following the discovery of the vulture restaurant perched fixes were obtained for Orange (14 fixes), Blue (19 fixes) and White (eight fixes) on 8, 11 and 6 days, respectively.

Periods C and D

All five vultures with functional tags were recorded within 6 km of the vulture restaurant while carcasses were available during provisioning period D, with White, Orange, Blue and Yellow recorded on 73, 61, 68 and 33 days, respectively, out of the 73 day period. Only a single fix was obtained for Green within 6 km of the restaurant, when it passed within 3 km at an altitude of 1,686 m on 15 June. Despite their proximity, none of the satellite-tagged vultures visited the restaurant during provisioning period D, suggesting a marked change in behaviour that was unrelated to the availability of food at the vulture restaurant. Other independent variables that obviously changed between periods B and D included the stage of the breeding season and dramatically increased ambient temperature.

The home-range of four of the tagged vultures was significantly greater during periods C and D than during A and B (Freidman test: $S = 9.24$, d.f. = 3 $P = 0.026$; Table 2). The one exception to this trend was Green, the only tagged bird that attempted to breed, which ranged most widely during period A and showed little variation from period B onward.

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Table 3. Mean daily distance moved, and mean daily number of airborne fixes received from satellite-tagged vultures for all calendar days during which 10 fixes or more were received (N), and all calendar days during which at least 10 three-dimensional fixes were received (n).

Tagged bird	Period	Mean distance moved ±SD (min.–max.), *n*	Mean airborne fixes ± SD (min.–max.), *n*
Blue	A	19.3 ± 11.9 (2.4–61.1), 46	1.9 ± 1.5 (0–5), 46
	B	12.8 ± 12.6 (1.5–58.9), 26	1.2 ± 1.2 (0–4), 27
	C	30.8 ± 24.5 (2.7–86.8), 61	2.9 ± 2.0 (0–7), 59
	D	41.4 ± 28.2 (6.9–161.6), 72	4.4 ± 1.5 (1–7), 73
White	A	13.1 ± 6.7 (2.4–29.7), 45	2.8 ± 1.5 (0–5), 45
	B	11.9 ± 5.1 (5.1–26.7), 20	1.8 ± 1.1 (0–4), 20
	C	25.5 ± 19.8 (0.2–75.4), 38	3.8 –± 1.9 (0–8), 38
	D	23.0 ± 17.3 (0.8–78.3), 69	4.0 ± 1.6 (0–7), 66
Orange	A	23.9 ± 18.1 (2.1–81.3), 45	3.1 ± 1.5 (0–6), 45
	B	23.5 ± 20.9 (1.6–79.8), 26	2.0 ± 1.6 (0–6), 26
	C	45.3 ± 35.0 (0.3–175.0), 69	3.6 ± 2.1 (0–8), 69
	D	45.9 ± 28.1 (0.7–156.8), 73	4.4 ± 2.0 (0–9), 73
Green	A	12.0 ± 16.0 (0.1–48.0), 15	1.6 ± 1.8 (0–4), 14
	B	22.5 ± 21.8 (0.1–68.6), 28	2.0 ± 1.7 (0–5), 26
	C	41.9 ± 21.3 (3.7–88.2), 70	5.2 ± 1.8 (1–9), 70
	D	48.3 ± 23.8 (4.8–128.3), 73	6.5 ± 1.8 (2–9), 73
Yellow	A	29.1 ± 20.8 (1.7–95.6), 23	2.5 ± 1.3 (0–5), 23
	B	52.5 ± 36.3 (1.3–11.8), 11	2.6 ± 1.9 (0–5), 12
	C	71.3 ± 49.7 (0.4–178.9), 54	4.1 ± 2.1 (0–9), 52
	D	72.7 ± 56.9 (0.1–226.3), 52	3.9 ± 2.1 (0–8), 50

Blue and White continued to roost in the vicinity of the vulture restaurant with 81% (n = 69) and 76% (n = 66) of identified roosts respectively within 6 km during period C and 78% (n = 73) and 92% (n = 73) during period D. Only 38% (n = 71) of Orange's and 3% (n = 69) of Yellow's roost positions were within 6 km of the vulture restaurant during period C and 33% (n = 73) and 35% (n = 63), respectively, during period D. Green did not roost within 6 km of the vulture restaurant at any time.

The mean daily distance moved was greater for all birds during the latter half of the study (Table 3), and each bird spent proportionately more time in flight during periods C and D than during periods A and B (Table 3) with up to nine hourly fixes per day received from flying vultures. This marked change in movement parameters again suggests that some other independent variable had a greater effect on movements in the latter half of the study period than food availability at the vulture restaurant.

Discussion

This study has demonstrated that the provisioning of uncontaminated food at vulture restaurants can reduce diclofenac-related mortality at a vulture colony. Mean daily mortality was shown to decline from 0.387 (41 vultures in 106 days) during control periods to 0.072 (8 vultures in 111 days). These comparisons are complicated by fluctuating numbers of vultures present in the colony between and during provisioning and control periods. However, mean daily mortality of 0.105 during provisioning period B (4 vultures in 38 days) was less than half the 0.225 in period C (16 birds in 71 days) when vulture numbers remained approximately stable. Furthermore, mean daily mortality was consistently lower during provisioning than control periods, indicating that vulture restaurants are able to reduce vulture mortality rates, irrespective of the number of birds in the colony.

The movements of tagged vultures indicated that the restaurant was also successful in modifying foraging behaviour, consistently reducing home-range, time in flight and mean daily distance travelled once the predictable food source had been located. However, as all tagged vultures were male and only one attempted to breed, it is not possible to determine whether these birds were representative of the breeding population. To address this question it would be necessary to tag a much larger sample size, or collect data over a longer period – options that are both cost-prohibitive. The possibilities exist, for example, that the presence of the GPS-PTT unit and patagial tag affected their breeding behaviour, or these birds may have been 'floaters' (Newton 1979) that would not have bred anyway but were otherwise more susceptible to being trapped. Despite these limitations the PTT units were successful in describing a range of foraging patterns and the modification of some of these by the vulture restaurant.

Even with the ready availability of uncontaminated carcasses during provisioning periods at least five dead vultures were found with visceral gout while the restaurant was operating. Although visceral gout is a non-specific finding indicative of renal failure and may have many causes, this remains significant in the context of vultures in South Asia. Analyses have confirmed that all 39 cases of visceral gout in *Gyps* vultures examined in Pakistan, India and Nepal contained residues of diclofenac (Oaks *et al.* 2004, Shultz *et al.* 2004). Visceral gout was found in 39 (97%) of the vultures examined in this study, which strongly suggests that diclofenac was the most important cause of death, including at least five vultures that died during provisioning periods.

In Punjab province, high densities of livestock have led to a ready supply of carcasses for foraging vultures. Even when vulture attendance at the restaurant was highest, the predictable food source was not sufficiently attractive to deter birds from utilizing carcasses encountered elsewhere. During the provisioning periods vultures were observed at livestock carcasses close to the restaurant site, indicating a continued, albeit lower risk of diclofenac exposure. Reasons for this may include intra-specific competition at the restaurant encouraging vultures to feed elsewhere, or preference for a more varied diet than that available at the restaurant. This could be tested by providing food at multiple sites, increasing the numbers of individual carcasses at each site and using a greater diversity of food species.

The restaurant was affected by seasonal variations in foraging behaviour, attracting few vultures and no tagged birds during the post-breeding period. At this time vultures spent an increasing proportion of time in flight, covered greater distances and occupied larger home-ranges. Nutrient requirements will decrease following breeding (Houston 1976) and observations of soaring vultures over the restaurant suggest that these movements were not entirely motivated by food. Diurnal temperatures regularly exceed 45°C during these months (Pakistan Meteorological Department, Lahore, unpubl.), and it is possible that thermoregulation may supersede foraging as the primary motivation for soaring, contributing to the seasonal disinterest in the restaurant.

The relative failure of the restaurant to attract vultures during the post-breeding period suggests that the provision of uncontaminated food was unrelated to the reduction in mean daily mortality at this time. There are several possible explanations that might explain this apparent paradox:

1. Seasonal variation in nutritional requirements may reduce feeding frequency and diclofenac encounter rates.
2. Seasonal variation in disease incidence or livestock management may lead to a reduction in diclofenac availability.
3. Seasonal variation in ranging patterns may lead to vultures dying far from the colony, masking true diclofenac exposure rates.

Each of these factors may contribute to some degree. The restaurant was most successful when energy demands were greatest, during the early nestling period (Houston 1976). Breeding success at Toawala during 2004 was only 40% (Gilbert *et al.* unpubl. data), so by the post-breeding period a large proportion of birds were no longer provisioning offspring. Also, seasonal increases in home-range size may have reduced the proportion of dead birds that could be located during mortality surveys. Irrespective of the reasons, vulture restaurants contribute little or nothing to reducing mortality during the hot months of the non-breeding period.

Individual variation in vulture ranging behaviour also greatly affected the restaurant's effectiveness in modifying foraging patterns. Although all vultures were trapped at Toawala, the home-range of just three was centred in the colony and amenable to modification by the vulture restaurant. The restaurant was unable to attract the only vulture that attempted to breed (Green), which nested at a distance of 27 km, or the bird that ranged widely utilizing multiple roost-sites across the province (Yellow). We can conclude that without the continual maintenance of multiple, widely dispersed provisioning sites it will only ever be possible to reduce diclofenac contamination in a subset of the total population that normally ranges near the restaurant.

This study has demonstrated that during the cool winter breeding season it was possible to modify vulture foraging behaviour and reduce mortality by provisioning a vulture restaurant with uncontaminated food. However, the restaurant was only able to modify the behaviour of vultures with home-ranges centred close by. The restaurant did not attract vultures during the non-breeding season when other factors, such as high ambient temperatures, may influence soaring behaviour and movement over large areas in which food was abundant and exposure to diclofenac-contaminated carcasses could occur. Even under optimum conditions it is not possible to eliminate diclofenac exposure entirely where alternative carcass sources are readily available. Supplementary feeding may prove to be a useful management tool for slowing declines locally in the short term. However, extinction is inevitable in all populations foraging in areas where diclofenac is in veterinary use and treated carcasses become vulture food at sufficient frequency to cause deaths and negative population growth. Elimination of diclofenac in veterinary use is the most certain way to prevent vulture deaths from diclofenac exposure, although education of veterinarians and livestock owners to avoid treatment of terminally ill livestock, or to bury or burn carcasses of recently treated livestock, may also be helpful.

Acknowledgements

The Peregrine Fund's Asian Vulture Crisis Project was supported by the Gordon and Betty Moore Foundation, The Peregrine Fund, Disney Wildlife Conservation Fund, Zoological Society of San Diego, UN Foundation, Summit and Ivorybill Foundations, and other important donors. We would like to thank the following individuals and organizations for their partnership, help and co-operation: the Ornithological Society of Pakistan (OSP), Nature Conservation Pakistan, Faisal Farid, Brigadier Mukhtar Ahmed, Punjab Department of Wildlife and Parks, National Council for the Conservation of Wildlife (NCCW), Bahauddin Zakariya University Multan, WWF-Pakistan, Zoological Society of San Diego, Washington State University, and University of Michigan.

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Received 7 June 2005; revision accepted 2 April 2006