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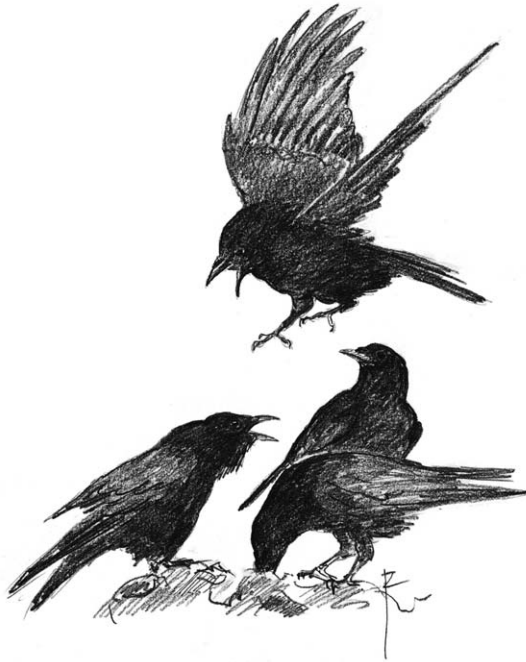
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Impact of focal food bonanzas on breeding Ravens *Corvus corax*

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Contrary to expectations, a manyfold increase in human-provided carcasses was paralleled by a near-total failure of breeding success in a small Raven *Corvus corax* population in the central Netherlands. Shot game and road casualties had been deposited at two to three point sources, where the bonanza was quickly monopolized by flocks of non-breeding Ravens. Breeding success improved substantially as soon as carcasses were dispersed throughout the terrain, enabling territorial pairs to profit from nutritious food without being outcompeted by non-breeding Ravens.

Key words: food distribution, rich food patch, floaters, depressed reproductive success

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In the early 20th century, the Raven *Corvus corax* was a scarce breeding bird in The Netherlands until human persecution did away with the last remaining pairs (Bijlsma *et al.* 2001). An extensive reintroduction programme in 1966–92 succeeded in establishing a small population in the late 1970s. Breeding numbers in The Netherlands remained consistently low till the mid-1980s, when numbers started to increase for a decade, to level off again from the early 1990s onwards (Bijlsma *et al.* 2001, Renssen & Vogel 2001). The present population is estimated to be 75–95 pairs, mostly concentrated in the wooded Veluwe region in the central Netherlands (www.sovon.nl).

The study area on the south-western Veluwe was colonised in 1978, since when numbers and breeding success have been monitored. In 2002, the policy regarding shot game and road casualties changed; instead of removing carcasses, these were discarded in the field to provide food for scavengers and a variety of other animals (Bosscher 2003). Ravens are quick to exploit and profit from anthropogenic food resources (Heinrich 1988, Rösner *et al.* 2005, White 2005, White 2006, Kristan & Boarman 2007, Dall & Wright 2009, Webb *et al.* 2011, Webb *et al.* 2012). We hypothesized that the boost in nutritious food should enhance breeding density and/or reproductive output of local Raven pairs nesting near point sources of carrion.

Study site and methods

From 1974 through 2012, the raptor and Raven populations of the nature reserve of Planken Wambuis (52°4'N, 5°44'E, 20 km² of woodland, heaths and arable land on sandy soils, managed by Vereniging Natuurmonumenten) and adjacent forests of Hindekamp, Hertenreservaat and Ginkelse Zand (managed by municipality of Ede), altogether some 35 km², were closely studied (Bijlsma 2004, Rutz & Bijlsma 2006; Figure 1). The management by Vereniging Natuurmonumenten of the local game population presented supplemental feeding opportunities for Ravens in a habitat otherwise poor in natural resources. Red Deer *Cervus elaphus* and Wild Boar *Sus scrofa* were being food-supplemented in winter with large but variable quantities of potatoes, apples, corn, beets and other plant matter. This food bonanza was also exploited by territorial Ravens. Game feeding reached a peak in 1989, when 119,000 kg of extra food was supplied, then was gradually reduced and finally, in 2002, completely banned except for an annual supply of 100–500 kg to attract game to specific sites (Figure 2).

Up to and including 2001, carcasses of shot game were removed, although entrails and lungs were discarded in the field. From 2002 onwards, shot animals and road-killed carrion were left behind in the terrain, concentrated at two or three focal points at any

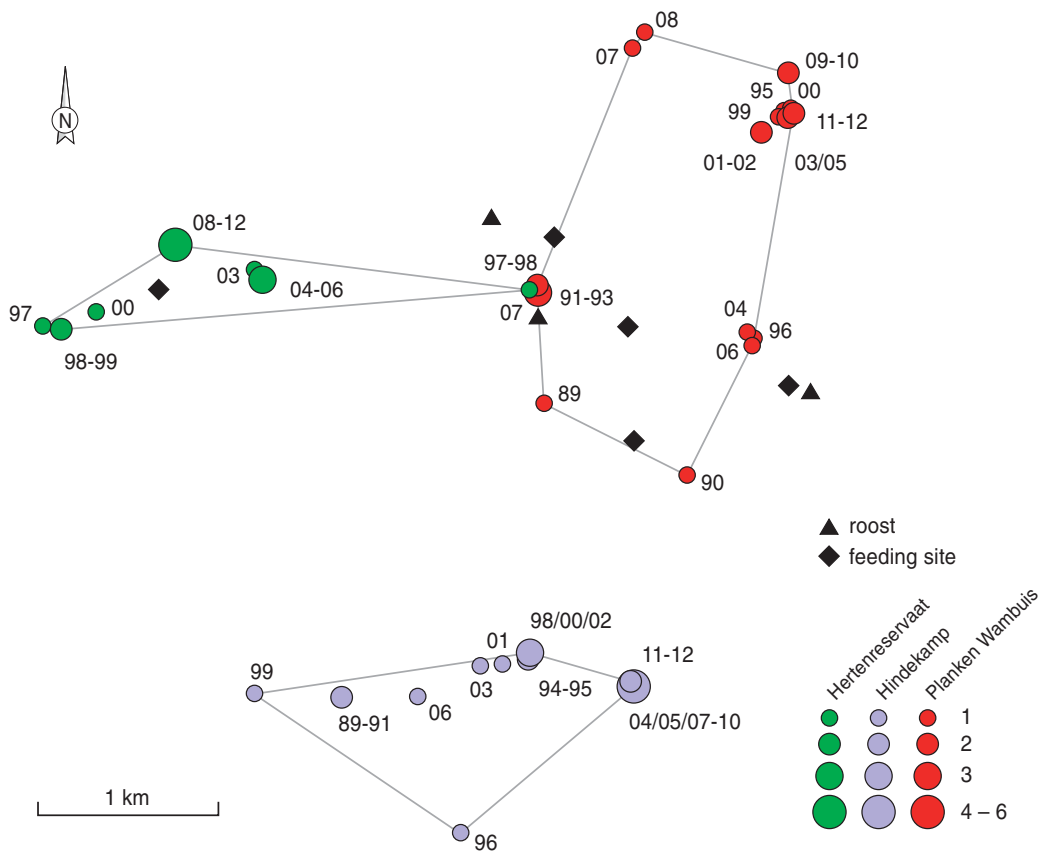


Figure 1. Successive nest sites in three territories in the study area in 1989–2012 (outlined with polygons), roosts of non-breeding flocks and focal food bonanzas in 2002–06.

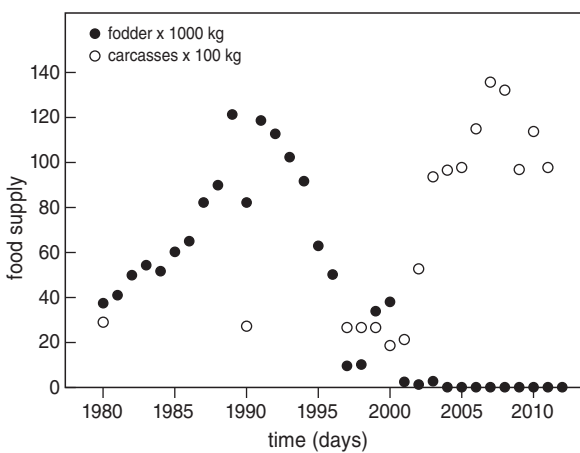


Figure 2. Supplemental feeding of ungulates and Wild Boars with plant material was standard practice in the 1980s and 1990s, then was gradually reduced to almost nil. Gutpiles generated by game hunting in winter provided high-quality food for Ravens in 1980–2001, but from 2002 onwards the entire carcass was discarded in the field.

one time (Figure 1). After 2006, carrion was scattered throughout the study area instead of concentrated at few point sources.

Plant (1980–2012) and animal (1980, 1990, 1997–2012) matter were weighed before being deposited at game feeding sites and carrion dumps (Figure 2). The availability of carcasses peaked in autumn and winter, in line with the shooting season; between 11 and 56% of the biomass was available between January and April, the main (pre-)breeding period of Ravens in our study area (mean start of laying 6 March, SD = 14, n = 50, range 18 February – 15 April).

As a proxy for chick condition, we classified the bare skin of Raven bellies as rimpled or not, i.e. an indication of being malnourished or well-fed respectively, using data collected once per nest at chick ages of 21–39 days old. Body mass cannot be used to assess condition, unless corrected for sex; morphometric sexing, however, proved impossible in chicks younger than 30 days old (R.G. Bijlsma, unpubl.).

Results

First breeding was recorded in 1978, and a single pair was present up to and including 1981. Between 1982 and 1985, Ravens were absent, but resettlement took place in 1986 (1 pair), since when numbers increased to 3 breeding pairs in 1998. Except for 2001/02, when 2 pairs were present, numbers remained stable at 3 pairs through 2012, i.e. did not increase when the availability of carcass biomass increased fourfold after 2001. The average density of 8.6 pairs/100 km² in Planken Wambuis and vicinity is typical for the south-western part of the Veluwe (in 2012, 8 pairs on 100 km²).

Reproductive output, measured as the mean number of fledglings produced per egg-laying pair, averaged 3.20 in 1989–96 (massive game feeding, gutpiles), 2.69 in 1997–2001 (game feeding strongly reduced, gutpiles), then declined to 0.21 in 2002–06 (game feeding banned, high carcass availability at focal sites), and increased to 2.50 from 2007 onwards (no game feeding, high carcass availability throughout the terrain) (Table 1).

Chick condition as evident from their bellies (rimpled or not) was particularly good in 1989–96 (none of 20 chicks in 5 nests had a rimpled belly) and in 2002–06 (but only 3 chicks in 2 nests). In 1997–2001 and in 2007–12, resp. 30.3% and 16.7% of young showed rimpled bellies (Table 1).

Discussion

In contrast to our expectation, the reproductive output of Ravens in the study area declined to almost nil as soon as the availability of carcasses substantially increased. Also, breeding density did not increase but remained stable. In the five-year period prior to the start of carcass supplementation (1997–2001), Ravens raised on average 2.69 young per nesting pair (and

even 3.20 in 1989–96, when game feeding was in full swing), which declined to 0.21 in 2002–06 (Table 1), the latter period typified by a substantial boost in nutritious food dumped at two or three point sources (two km apart, Figure 1). In 2002–06, only 2 out of 14 pairs succeeded in raising chicks to fledging, i.e. 1 chick in 2002 and 2 chicks in 2003. Failures occurred during the egg stage (6×) and early chick stage (2×); in four cases it was impossible to decide whether eggs had been laid. Causes of failure remained a mystery.

Persistent food bonanzas, of anthropogenic origin or not, are known to attract non-breeding Ravens from afar, resulting in improved juvenile survival (Webb *et al.* 2004), an increase in nest density and fledging success (Kristan & Boarman 2007), a higher nest density but poorer fledging success (Grünkorn 1999), and a higher spring abundance and nest density (White 2006). In our study area, however, neither density nor reproductive output improved after carcass biomass was boosted substantially. The steep decline in nesting success in 2002–06 may have been associated with non-breeding groups, whose persistent presence at focal carcass dumps seemed to deter territorial pairs from using this abundant food source, and may have increased the frequency of territorial disputes, or may have enhanced diseases and parasites. A negative effect of high numbers of non-breeders on the breeding success of neighbouring pairs was also recorded near two landfills in northern Germany (Grünkorn 1999, Lo & Müller 2000). Experiments by Heinrich (1988) showed that resident territorial adults defended prized food bonanzas, but could be outcompeted by juvenile non-breeders that were able to neutralize aggressive adults by vigorously recruiting non-territorial vagrants to carcass bonanzas. In our study, anecdotal information on the foraging behaviour of territorial pairs suggested that breeding adults avoided carcass dumps

Table 1. Number and condition of Raven fledglings in the study area during four periods with varying types and quantities of supplemental food (see Figure 2). Carrion availability for 1989–1996 is based on 1990 only. Condition is expressed as proportion of chicks with rimpled bellies.

Period	Supplemental food (kg)				Fledglings/breeding pair			Condition		
	Plant		Carcasses		Mean	SD	Number of nests	% rimpled	Number of chicks	Number of nests
	Mean	SD	Mean	SD						
1989–1996	91,257	240	2648	-	3.20	1.21	14	0.0	20	5
1997–2001	17,860	144	2274	328	2.69	1.94	13	30.3	33	8
2002–2006	760	606	8992	2049	0.21	0.56	14	0.0	3	2
2007–2012	158	67	10,121	2912	2.50	1.74	18	16.7	44	12

that were monopolized by non-breeders, and instead roamed widely in search of food. Pellet contents further indicated that a wide range of food types was utilized, from cereals and insects to eggs, birds, mammals and carrion. Chicks were mostly fed with fresh red meat, as evident from regurgitated food items obtained from chicks fitted with a narrow neck-ring (Bijlsma 2004). Where carcass bonanzas were predictable, Raven flocks of 27–70 non-breeding birds stayed for prolonged periods of time in winter and spring (August through April), with occasional visits of smaller flocks in May and July. These birds often roosted within 100–500 m of point sources of carrion and were a source of conflict for territorial Raven pairs and local raptors. This strategy is well-known among Ravens, and supposedly improves juvenile survival (Webb *et al.* 2004).

To discourage monopolization of carcass bonanzas by non-breeding flocks of Ravens, and to present breeding Ravens with an opportunity to access high-quality food, shot game and road-killed carrion were more widely dispersed across Planken Wambuis from 2007 onwards. Reproduction improved at once, especially noteworthy as none of the three pairs had succeeded in raising fledglings in the three preceding years. In 2007–12, only four breeding attempts failed and the remaining 14 breeding attempts resulted in 45 fledglings (on average 2.5 fledglings/pair, Table 1). It is tempting to suggest that the improved nesting success resulted from the change in the strategy of carcass distribution (dispersed rather than focal) and the subsequent disappearance of non-breeders. In fact, after 2006, territorial Ravens were recorded foraging at solitary carcasses across the terrain, in contrast to the period of 2002–06 when carcasses were concentrated at two to three dumps where they were monopolized by non-breeders. An alternative explanation for the improved nesting success after 2006 may have been ageing of local breeding pairs. Although no information is available on lifetime reproductive success in Ravens, other long-lived species are known to improve their fitness prospects with age (Newton 1989). However, pre-2002 reproductive output was similar or even better than in the post 2006-period, suggesting that poor reproduction in the intervening period was a temporary dip unassociated with food supply per se. Apparently, non-breeders can successfully displace territorial pairs from food resources when bonanzas are localised, predictable and persistent in time, which – perhaps in combination with increased interference – decidedly depressed the breeding performance of territorial pairs.

Vereniging Natuurmonumenten was instrumental in distributing carcasses. The late Thom Renssen, Mr. Raven par excellence, is sorely missed. Two anonymous referees improved the manuscript.

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Samenvatting

Nadat Raven *Corvus corax* in de vorige eeuw waren uitgeroeid, moest er een herintroductie aan te pas komen alvorens de soort zich in de jaren zeventig opnieuw als broedvogel in Nederland vestigde. Op Planken Wambuis en omgeving, ZW-Veluwe, werd het eerste broedpaar in 1978 vastgesteld. Vanaf 1998 zaten hier permanent drie paren op 35 km², met uitzondering van 2001–02 (twee paren), een dichtheid die overeenkomt met die van de ZW-Veluwe als geheel (in 2012: 8 paren op 100 km²). In het studiegebied leven forse aantallen Edelherten *Cervus elaphus* en Wilde Zwijnen *Sus scrofa*, die tot en met 2001 werden bijgevoerd met aardappels, appels, korrelmaïs, bieten en brokken. Daarvan werd ook door de Raven gegeten. Van het geschoten wild bleven tot en met 2001 de ingewanden en longen in het veld achter, een gewilde voedselbron van Raven; de kadavers werden echter afgevoerd. In 2002 veranderde het lokale wildbeleid: met bijvoeren werd gestopt, en het geschoten wild werd op enkele vaste plekken in het terrein achtergelaten. Dat betekende gemiddeld een verviervoudiging van hoogwaardig voedsel voor

Raven in winter en voorjaar. Op grond daarvan verwachtten we een toename van de broeddichtheid en/of een verbetering van het broedsucces. Niets bleek minder waar: de dichtheid bleef gelijk en het broedsucces zakte naar het nulpunt. De vermoedelijke oorzaak was dat de kadaverbonanza door groepen niet-broedende Raven werd gemonopoliseerd. Deze groepen zorgden bovendien voor onrust bij de territoriale paren. Pas toen in 2007 werd besloten de kadavers willekeurig verspreid in het terrein achter te laten, in plaats van te dumpen op enkele vaste locaties, wisten de broedende Raven weer jongen groot te brengen. Het leek erop dat de niet-broedende Raven door de gewijzigde strategie geen kans zagen het voedsel te monopoliseren, waardoor het weer beschikbaar kwam voor de territoriale paren. Bovendien verdwenen de groepen niet-broeders, of bleven ze slechts kort hangen, waardoor de onrust rond broedplaatsen afnam.

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