~110,000 to ~85,000 years ago, during which FB-δ^{15}N rises but there is no clear sign of an increase in Subantarctic productivity (Fig. 2).

The coincidence of the dust and productivity increases with the latter half of the CO_2 draw-down over the last ice age has been widely noted (*15*, *17*, *35*). Model simulations suggest that iron-driven drawdown of major nutrients in the Sub-antarctic can drive this 40-ppm portion of the ice age CO_2 decline without violating other constraints, such as those involving deep ocean calcite satu-ration state and the $^{13}C/^{12}C$ ratio of dissolved in-organic carbon (*12*). Our confirmation of iron fertilization in MIS 6 (prior to 130,000 years in our data) and in MIS 4–MIS 2 validates this long-held hypothesis for glacial-interglacial CO_2 change. The nearly complete nitrate drawdown estimated for Site 1090 is actually greater than required to explain 40 ppm of CO_2 decline, were this location representative of global Subantarctic Mode Water formation (*24*). However, Subantarctic Mode Water forms further south near the Subantarctic Front (*36*), where the peak ice age nitrate con-centration may have been higher. Moreover, the Pacific sector of the Subantarctic may have ex-perienced weaker iron fertilization, given lower ice age dust fluxes there (*37*). Nonetheless, we expect that ice age Subantarctic FB-δ^{15}N elevation ap-plies to all sectors of the Southern Ocean because, even with strong zonal changes in dust deposition, the rapid eastward flow of the Circumpolar Current would weaken zonal gradients in nitrate concen-tration and δ^{15}N. This expectation appears to be consistent with the available DB-δ^{15}N data (*24*).

With improvements in the ice core recon-structions, it has become clear that each of the millennial cold spells in Antarctica was associated with both an increase in dust flux to Antarctica and a decline in atmospheric CO_2 (Fig. 3). Our results indicate that these millennial-scale events were also associated with higher dust flux to the Atlantic Subantarctic, higher productivity, and fi-

nally more complete nitrate consumption (Fig. 3). Although attention has recently been focused on Antarctic overturning changes as the underlying cause of the millennial-scale CO_2 changes (*38*, *39*), the Site 1090 data suggest that Subantarctic iron fertilization can also explain them. This raises the possibility that the millennial-scale CO_2 oscil-lations are caused by the two Southern Ocean mechanisms working in concert; a similar mecha-nism has been proposed to achieve the full ice age drawdown in atmospheric CO_2 (*13*).

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From Parasitism to Mutualism: Unexpected Interactions Between a Cuckoo and Its Host

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Avian brood parasites lay eggs in the nests of other birds, which raise the unrelated chicks and typically suffer partial or complete loss of their own brood. However, carrion crows *Corvus corone corone* can benefit from parasitism by the great spotted cuckoo *Clamator glandarius*. Parasitized nests have lower rates of predation-induced failure due to production of a repellent secretion by cuckoo chicks, but among nests that are successful, those with cuckoo chicks fledge fewer crows. The outcome of these counterbalancing effects fluctuates between parasitism and mutualism each season, depending on the intensity of predation pressure.

Interspecific avian brood parasites generally harm their hosts in two main ways: Evicting parasites eject all other eggs and hatchlings from the nest, whereas nonevicting parasites are raised alongside host offspring but usually outcompete some or all of them for food (*1*).

Specific defenses against brood parasites, in-cluding ejection of alien eggs and mobbing of parasitic adults (*2*), have evolved in many but not all host species (*3*). It has been hypothe-sized that lack of defenses may be due to rel-atively recent contact between the antagonistic species or to hosts refraining from exhibiting their defenses when costs outweigh benefits (*1*). Alternatively, defenses might not evolve if brood parasite-host interactions can switch to a mutual-ism, as suggested by Smith (*4*). His results from a study on giant cowbirds (*Scaphidura oryzivora*),

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however, were never replicated (5), and brood parasite-host systems still represent a paradigm of parasitic interactions. Here we show, in a system different from Smith's, that a brood parasite can indeed provide a benefit to its host.

The great spotted cuckoo (*Clamator glandarius*) is a nonevicting brood parasite specialized on corvids, mainly magpies (*Pica pica*) and carrion crows (*Corvus corone corone*) (6, 7). Cuckoos strongly reduce magpie reproductive success (6), but apparently this does not occur in crows, whose larger offspring are often raised alongside the parasite (7, 8). Unlike magpies, crow parents do not evict alien eggs or mob parasitic adults in proximity of the nest (9). In our study area in northern Spain (42°37′N, 5°26′W), the great spotted cuckoo can parasitize up to 67.7% of crow nests (8).

We investigated (i) whether the great spotted cuckoo provides a benefit to crows and whether such benefit could derive from the ability of cuckoo chicks to deter predators with a noxious secretion that they release when harassed, as well as (ii) whether the outcome of host-parasite interaction varies across seasons, depending on the intensity of predator pressure. To do so, we used data collected over 16 years to analyze the effect of the parasite on crow reproductive success. In the studied population, crows breed cooperatively and raise a single annual brood, although they can renest in case of early nest failure (10, 11). Each season, nests were monitored to record laying date, clutch size, presence of parasitic eggs, hatching success, and number of fledglings produced (*n* = 741 nests in 109 territories) (11). To test whether crow clutches benefit from being parasitized, we transferred cuckoo hatchlings (one or two per nest) into synchronous nonparasitized nests (average difference in laying date of the first egg ± SE = 0.54 ± 0.23 days), whereas unmanipulated parasitized and nonparasitized nests served as controls (11). Furthermore, to control for the effect of the manipulation (adding or removing chicks), in a subsequent

experiment we moved one crow chick between synchronous nonparasitized nests and kept unmanipulated nests for control (11). Finally, we used gas chromatography and mass spectrometry to analyze the chemical composition of cuckoo cloacal secretions, and we performed repellence tests on species belonging to the three main groups of crow nest predators (that is, mammals, corvids, and raptor birds) (11, 12). Seventeen quasi-feral cats (that is, free-ranging cats that hunt year-round but could be attracted with food) were each presented with 10 pieces of chicken meat, treated either with water or natural cuckoo secretion. Seven captive crows and seven captive raptors were each offered six pieces of meat (three treated and three control), one at a time.

Our analyses of the long-term data set (11) show that the seeming lack of cost of raising cuckoos on crow reproductive success resulted from the combination of two counterbalancing effects. Parasitized and nonparasitized nests had similar probability of reaching the hatching stage [0.771 and 0.731, respectively; *z* score (*z*) = 0.264, *P* = 0.792, *n* = 741] (table S1). Once the eggs hatched, parasitized nests were more successful (that is, more likely to produce at least one crow fledgling) as compared with nonparasitized nests (probability of success = 0.764 and 0.538, respectively; *z* = 2.94, *P* = 0.003, *n* = 550) (table S1). However, among nests that were successful, those containing a cuckoo chick produced fewer crow fledglings than those without cuckoos (average ± SE = 2.073 ± 0.139 and 2.564 ± 0.064, respectively; *z* = –2.670, *P* = 0.008, *n* = 312) (table S1). Overall, throughout the 16 seasons, parasitized and nonparasitized broods did not significantly differ in the number of crows fledged (1.584 ± 0.149 versus 1.379 ± 0.068, respectively; *z* = 0.390, *P* = 0.694, *n* = 550), though results suggest a slight benefit from raising a cuckoo.

The results of the translocation experiment show a causal link between the presence of a parasitic chick and greater nest success. Among parasitized nests, those from which cuckoos were
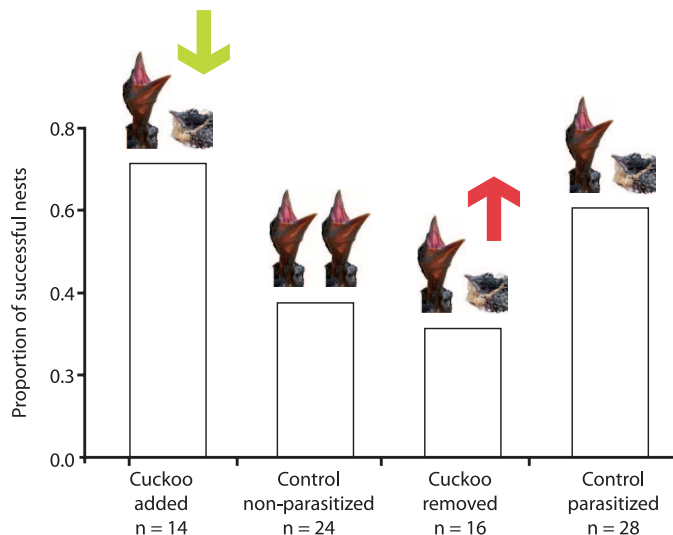
removed failed significantly more often than control nests (probability of success = 0.312 and 0.607, respectively; *z* = –2.065, *P* = 0.039) (Fig. 1 and table S2), whereas among nonparasitized nests, the addition of cuckoo chicks resulted in significantly increased success (unmanipulated nonparasitized = 0.375, cuckoo added = 0.714; *z* = 1.984, *P* = 0.047) (Fig. 1 and table S2). In sharp contrast to the effect of cuckoo chick transfer, nests in which a crow chick was added showed no difference in success rate (0.364, *n* = 11) from those that were not manipulated or those from which a crow chick was removed (0.818 and 0.727, respectively; *n* = 11 for both treatments; *z* = 1.707, *P* = 0.088 and *z* = 1.785, *P* = 0.074) (table S2), though the difference was suggestive of a reduction.

The most plausible mechanism driving the reduction of failure in nests with cuckoos is predator repellence by a malodorous cloacal secretion that parasitic chicks void when grabbed (supplementary text). This secretion is only produced by cuckoo nestlings (0 of 23 captured adults showed it) and can be copious (up to 1.2 ml released by a 45-g chick; average ± SE = 0.93 ± 0.06 ml, *n* = 8). When handling chicks, we observed voiding of the secretion in 20.8% of hatchlings (1 to 2 days old, *n* = 24), 71% of nestlings of 3 to 4 days (*n* = 21), and 90% of chicks older than 4 days (*n* = 59). At fledging, voiding of the secretion became less frequent (only two of six handled fledglings produced it).

The chemical analysis of cuckoo secretion revealed a mix of caustic and repulsive compounds, dominated by acids, indoles, phenols, and several sulfur containing compounds (Fig. 2) that are known to repel mammals and birds (13–16). Further chemical analyses confirmed the distinct volatile profile of a cuckoo's secretion as compared with feces of both cuckoos and crows, and its defensive function was confirmed by repellence tests. Eight of nine cats ate all 10 pieces of control meat, whereas only one of eight cats took a bite from treated meat (Fisher's Exact test, *P* = 0.01). When we reversed the treatment for 9 of the original 17 cats, those offered control meat (*n* = 5) ate all the pieces, but none bit the treated meat (*n* = 4; Fisher's Exact test, *P* < 0.01). Crows also showed avoidance of the treated meat (proportion of eaten/cached control and treated items = 0.524 and 0.150, respectively; *z* = –2.432, *P* = 0.008, *n* = 7) (table S3), as did the raptors (proportion of eaten control and treated items = 0.952 and 0.286. respectively; *z* = –3.355, *P* = 0.001) (table S3).,

Our study area hosts a large community of avian and mammalian nest predators (11) that causes failure of 21.2 to 78% of breeding attempts annually (10). In our experimental sample, unmistakable signs of predation (presence of broken feathers and/or damage of nest lining) were found in 10 of 21 nests that were inspected closely after failure. Overall, the analyses of long-term data, the translocation experiment, the repellence tests,

Fig. 1. Probability of success of experimental and control nests. n, number of nests.

Cuckoo added n = 14	Control non-parasitized n = 24	Cuckoo removed n = 16	Control parasitized n = 28

and the chemical analyses imply that the cuckoo contributes to nest success by repelling predators. We believe that the outcome of this parasite-host interaction may depend on predator pressure and thus fluctuates among parasitism, commensalism, and mutualism. Long-term data fit this condition-dependent scenario. Whereas cuckoos decrease host reproductive success at low rates of nest failure (which is a suitable proxy of nest predation rate) [17], parasitized nests produced more fledglings than nonparasitized nests during breeding seasons with high nest predation (Spearman's rank correlation coefficient $R = 0.834$, $n = 16$, $P < 0.001$) (Fig. 3).

It can be argued that provisioning the cuckoo chicks may still harm the crow host by worsening the quality of its own offspring or by demanding for an exaggerated amount of care, and that these costs eventually outbalance any benefit that the parasite can provide. However, we found that (i) crow fledglings raised alongside cuckoos were not in poorer conditions compared with those brought up in absence of parasites (weight/tarsus^3 ± SE with cuckoos = 2.06 ± 0.009, without cuckoos = 2.01 ± 0.004; $t = 1.178$, df = 315, $P = 0.240$, $n = 386$) (table S4), and (ii) raising a

cuckoo chick required substantially less effort than rearing a crow chick, as can be expected given the smaller size of the parasitic nestlings (approximately one-third of the weight of a crow) [18]. After controlling for total brood size (crows and cuckoos), broods containing cuckoo chicks required significantly fewer visits per hour than nonparasitized broods ($t = -2.637$, df = 20, $P = 0.016$, $n = 27$) (table S5). In addition, the total dependence period (nestling and postfledging) is shorter for cuckoos [19] than for crows [20]. The analysis of data for 89 crow parents (61 males and 28 females) confirmed that raising cuckoos had no significant consequences on annual adult survival (probability of survival of parasitized adults = 0.821, nonparasitized = 0.727; $z = 1.355$, $P = 0.175$) (table S6). Moreover, parasitized parents did not have significantly lower reproductive success in the following year (average number of fledglings ± SE = 0.818 ± 0.234 and 0.848 ± 0.110 for parasitized and nonparasitized adults, respectively; $z = -0.250$, $P = 0.803$, $n = 45$ males and 18 females) (table S7).

It has been advocated that interspecific interactions should not be strictly categorized as parasitism, commensalism, or mutualism [21],

because costs and benefits for each partner may vary in space and time, producing variable outcomes depending on the environmental context [for example, seed predation and dispersal [22] and cleaning symbioses [23]]. Here, we demonstrated that the consequences of brood parasitism can be beneficial (supplementary text) and that this benefit may be context-dependent, possibly preventing the evolution of host defenses, particularly when a nonevicting cuckoo parasitizes a larger host.
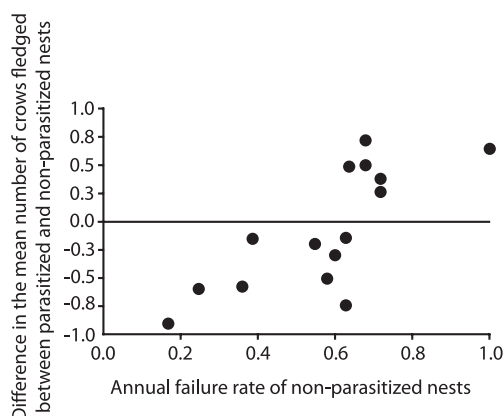
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Fig. 2. Chromatogram of the volatiles of cuckoo nestling secretion. 1, acetic acid; 2, propanoic acid; 3, dimethyl disulfide; 4, iso-butyric acid; 5, butyric acid; 6, pivalic acid; 7, isovaleric acid; 8, 2-methylbutanoic acid; 9, valeric acid; 10, α-pinene; 11, dimethyl trisulfide; 12, phenol; 13, caproic acid; 14, 3-carene; 15, acetophenone; 16, p-cresol; 17, 2-nonanone; 18, camphor; 19, dimethyl tetrasulfide; 20, indole; 21, skatole; 22, 2-dodecen-1-ol; 23, cyclic hexaatomic sulfur; 24, geranyl phenylacetate; 25, 2-tridecanone. Asterisks denote air contaminants, plasticizers, etc. Relative abundance is measured in number of ions.
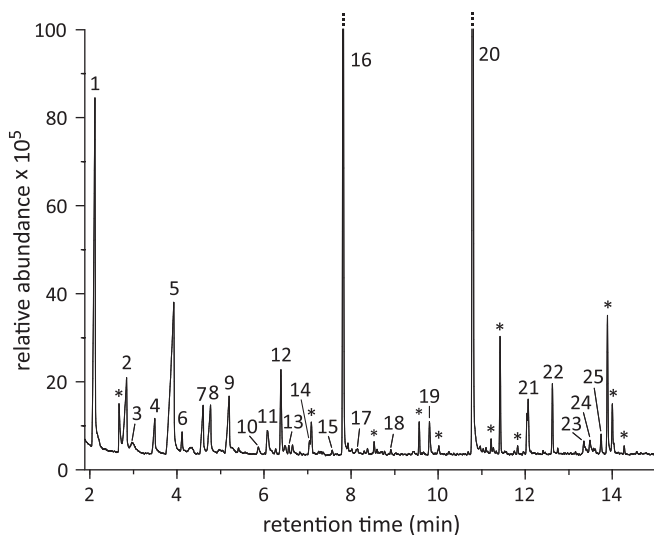
Fig. 3. Annual difference in the mean number of crows fledged between parasitized and nonparasitized nests plotted against annual failure rate of nonparasitized nests (proxy of nest predation rate). Above the zero line, the host benefits from the presence of the cuckoo.