based on combined radar and optical data, in which the high-precision radar astrometry had mitigated the effect of biased optical data. The corrected and extended set of data referred to here includes 145 optical, eight time-delay, and five Doppler measurements. When we included the refined astrometry, the estimated impact probability increased slightly to 0.33%.

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20. Some smaller factors examined include the mass of the Sun decreasing at a rate of -5.76×10^9 kg s^{-1} because of luminosity and particle emission [J. R. Jokipii, C. P. Sonnett, S. Giampapa, Eds., *Cosmic Winds and the Heliosphere* (Univ. of Arizona Press, Tucson, AZ, 1989)]. For the case of negligible matter infall, numerical integration shows that this solar mass loss rate causes a +13300-km along-track change in the orbit of 1950 DA by 2880 (a +16-min change in arrival at the intersection with the orbit of Earth). Galactic tidal perturbations [J. Heisler, S. Tremaine, *Icarus* **65**, 13 (1986)] are dominated by the distribution of mass within 300 parsecs of the solar system [K. A. Innanen, *Earth Moon Planets* **72**, 1 (1996)]. Inclusion of this acceleration in a numerical integration reveals a −8400-km along-track change in the orbit of 1950 DA by 2880, producing a −10-min change in the arrival timing. Galactic tidal acceleration ($\sim 10^{-15}$ mm s^{-2}) is three orders of magnitude greater than solar particle wind pressure acceleration at 1 AU but six orders of magnitude less than that of solar radiation pressure. These accelerations, although small, alter 1950 DA planetary encounter circumstances, resulting in a gravitationally amplified effect on the trajectory after 879 years. For comparison, the position of Mars, having no planetary encounters, changes only −85 km as a result of solar mass loss through 2880. With an 80% chance that 1950 DA has dynamically migrated from the inner main belt into its current Earth-crossing orbit (W. F. Bottke, personal communication, 31 May 2001), it is unlikely to experience cometary outgassing accelerations.
21. The Yarkovsky effect has been observed affecting spacecraft motion and is potentially significant for long-term asteroid motion. It is a function of the mass, size, shape, spin state, and global distribution of surface optical and thermal properties of an object. For Yarkovsky calculations, we used the OrbFit Yarkovsky model and software [D. Vokrouhlický, A. Milani, S. R. Chesley, *Icarus* **148**, 118 (2000)].
22. Our integrations are normally performed in 64-bit floating-point arithmetic ("double-precision") using a variable order, variable multistep, Adams-Krogh integrator, with local error tolerances of 10^{-14} and a maximum predictor/corrector order of 14/15. To reveal the cumulative machine numerical error in this approach, we integrated a reference trajectory using much slower but more precise 128-bit arithmetic ("quadruple-precision"), with local error tolerances of 10^{-19} and a maximum 21/22 order predictor/corrector. The quadruple-precision trajectory was then differenced with the double-precision trajectory to assess numerical error in the faster double-precision integrations.
23. An asteroid's PIN $= \Sigma LN\delta$, where L is the orbit perimeter length (9.953328 AU for 1950 DA); $N = (\tau_m - \tau_e)/p$, the map time minus the encounter time, divided by the orbit period (the number of orbits between the encounter and the 2880 map time); and $\delta = 2\tan^{-1}(GM_s v^{-2} d^{-1})$, the deflection angle due to the close approach, where G is the gravitational constant, M_s the mass of the two bodies, v their relative speed, and d the minimum approach distance. The masses of perturbing asteroids were approximated by assuming a bulk density of 3 g cm^{-3}, a diameter (in km) based on the absolute visual magnitude H_v, an albedo (p_v) common for the spectral type of the object, and the relation $\log_{10} p_v = 6.259 - 2\log_{10} D_{eff} - 0.4H_v$ [E. Bowell *et al.*, in *Asteroids II*, R. P. Binzel, T. Gehrels, M. S. Matthews, Eds. (Univ. of Arizona Press, Tucson, AZ, 1989), p. 551].
24. Asteroid 10 Hygiea was the most significant perturber other than Ceres, Pallas, and Vesta. Despite an average approach distance of 1.0 AU, 42 such Hygeia encounters with a mean relative speed of 3.9 km s^{-1} cause 19.8% of the total perturbation detected. This is 2.7 times the total effect of the next biggest perturber, 704 Interamnia. The single greatest perturbation is from a 0.003261-AU approach by 78 Diana on 5 August 2150. Asteroid 4217 Engelhardt approaches 1950 DA most closely, in 2736, at 0.001723 AU (~0.7 lunar distances), but the cumulative perturbative effect by 2880 is negligible.
25. With an optically determined synodic rotation period of 2.1216 ± 0.0001 hours, 1950 DA is one of the fastest known rotators among objects that large. See also *IAU Circular 7735* regarding asteroid 2001 OE84 [P. Pravec, personal communication, 12 August 2001; L. Šarounová, Ondřejov NEO Photometric Program (http://sunkl.asu.cas.cz/~ppravec/neo.htm)].
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28. The instantaneous acceleration due to solar radiation pressure was modeled as $d^2\mathbf{r}/dt^2 = (C_1 m^{-1} |\mathbf{r}|^{-2})\mathbf{F}$, where $\mathbf{r}$ is the Sun-to-Earth position vector, C_1 is a solar flux constant at 1 AU (2.27545×10^{-7} kg AU^3 m^{-2} day^{-2}), m is the mass of the asteroid, and $\mathbf{F}$ is a vector of geometric reflectivities (here, the exposed half-sphere surface area scaled by a reflectivity factor of $1 + p_v$, acting in the radial direction only).
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30. We are grateful to V. Negrón, A. Hine, and the staff of the Arecibo Observatory, as well as F. Krogh for his valuable insights and suggestions regarding numerical integration. Part of this research was conducted at JPL, California Institute of Technology (Caltech), under contract NASA. The Arecibo Observatory is part of the National Astronomy and Ionosphere Center, which is operated by Cornell University under a cooperative agreement with NSF and with support from NASA. Astrometric plate reduction work was supported by an NSF grant. Some of our Arecibo observations were obtained with the Caltech Baseband Recorder, whose development and fabrication were funded by NSF.

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Evidence for the Effect of Learning on Timing of Reproduction in Blue Tits

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We experimentally show that in blue tits (*Parus caeruleus*) egg-laying date is causally linked to experience in the previous year. Females that received additional food in the nestling period in one year laid eggs later in the next year compared with the control birds, whatever the degree of synchronization with the natural food abundance in the previous year. As a result, they raised their brood much later than the peak period of nestling food availability in the next year. The response to experience is adaptive for blue tits, which live in heterogeneous habitats where the peak period of food varies, but once settled will breed at the same location for life.

In birds, the degree of synchrony of the breeding cycle with the period of maximum food abundance for nestlings is crucial to the condition and survival probability of the offspring (*1*, *2*). Because reproduction starts much earlier than the time of maximum food requirement of the offspring, we expect birds to start reproduction in response to cues that predict the time of maximum food abundance. A number of such cues have been suggested, including day length, temperature, food abundance at the time of egg production, and phenology of the vegetation (*3*–*5*). However, all these studies emphasize the im-

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portance of current environmental factors in determining phenotypic plasticity of laying date. A study on great tits (*Parus major*) (*6*) suggested that laying dates were also affected by the feeding conditions experienced by the females in the previous year, but direct causal evidence was lacking. The apparent response could be the result of a correlation of an unknown factor related to both past experience (synchronization with the peak period of food availability) and laying date.

To seek causal evidence for an effect of past feeding conditions on laying date, we conducted an experiment with blue tits (*P. caeruleus*) in a Netherlands forest. We supplemented half of our experimental pairs with insect larvae throughout the nestling period (*7*, *8*), whereas the other half of the pairs served as a control. We provided one half of the estimated food amount consumed by blue tit nestlings (*9*). At the same time, we collected caterpillar frass during the breeding season (*10*) and estimated caterpillar biomass using the formula of Tinbergen and Dietz (*11*, *12*). We then looked at the response of the females that survived and bred the following year. In an attempt to remove energy and nutrient constraints on egg laying (*13*, *14*), we supplemented all blue tits (including those that served as a control in the nestling period) with food at the time of egg laying, both in the years with experimental food provisioning in the nestling period and those in which the response was measured [see supplemental material (*15*)]. In this way, females would be more responsive to the potential environmental cues at that time rather than delay laying due to resource constraints (*3*). (Throughout the text, we refer to food-supplemented birds as those that received food when raising their brood.)

We used the method described by Nager and van Noordwijk (*6*) to assess the between-year change in laying date of individual females independent of the change in laying date of the neighbors (*16*). Our main prediction was that females receiving additional food in the nestling period should not change laying date in the next year because their nestling period was synchronized with the peak period of food abundance, whereas controls, which (in our area) breed too late in their first year to be synchronized with the natural caterpillar peak, were expected to advance their laying date in the second year.

Supplementing food during the nestling phase clearly affected laying date in the next year: the food-supplemented females laid eggs later compared with the control birds, whatever the degree of synchronization with the natural food abundance in the previous year (Fig. 1; effect of treatment, $F_{1,12}$ = 28.79, P = 0.0002 after controlling for degree of synchronization in the year of experiment). For food-supplemented birds, which were predicted not to change their laying date, we found a slight delay of their laying date as well as an effect of the degree of synchronization with the natural food abundance. This could be because food was supplied at an increasing amount until day 10, after which the amount remained constant and might have been experienced as a late food peak. The slight delay in laying date in the next year was opposite from expected if the supplemented food had advanced laying date via an improvement of the nutritional status or a reduced work rate of the females [see supplemental material (*15*) for a potential indirect effect of food addition on the delay of egg laying].

Because females that were food-supplemented did not adjust laying date according to their synchronization with natural food abundance, they were expected to be, on average, less synchronized than control females in the next year. Given that in our experiment the food-supplemented birds slightly delayed their laying date, they were expected to be, on average, too late for the natural food peak. In the experimental year, the degree of synchronization did not differ between food-supplemented and control females, but in the following year food-supplemented females were more out of synchrony with the caterpillar peak than the controls (Table 1 and Fig. 2). Thus, food provisioning during the nestling phase led to mistiming of breeding the next year. This strongly suggests that the synchrony between the timing of the brood and the natural food availability experienced by the female is involved in the fine-tuning of the timing of reproduction in tits in an adaptive manner.

The results of this study may be viewed as an aspect of a more general strategy, where organisms recalibrate their "decision rule"

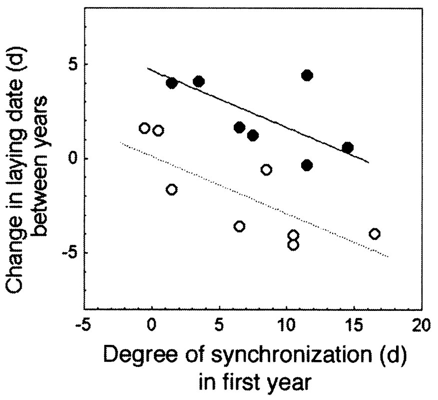

Fig. 1. Effect of food supplementation on change in laying date of individual female blue tits from year 1 to year 2, against the synchronization between their brood and peak caterpillar abundance in year 1 for the Hoge Veluwe from 1997 to 1999. The change in laying date was corrected for the change between years in the common environment by correcting laying date of the focal individual relative to neighbors (*16*). Open circles and broken line, control females; solid circles and solid line, food-supplemented females. The negative relation between past synchronization and change in laying date is consistent with the findings of Nager and van Noordwijk (*6*) in the great tit (effect of synchronization, $F_{1,12}$ = 13.00 and P = 0.004). The degree of synchronization did not differ between experimental groups in the year of food addition (Table 1).

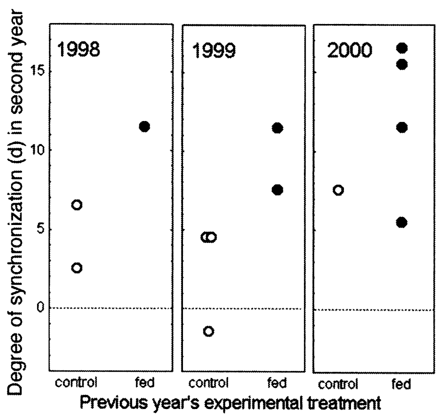

Fig. 2. Effect of food supplementation on the degree of synchronization between tits' breeding time and caterpillar peak date in the year following the experiment against the treatment in the experimental year. The dotted line indicates caterpillar peak date falling in the middle of the nestling period. In the three study years, most broods were late relative to the caterpillars (positive values of synchronization). Open circles, control females; solid circles, food-supplemented females.

Table 1. Degree of synchronization, expressed in days, between blue tits' breeding season and caterpillars (*16*), in the year of the feeding experiment (year 1) and in the following year (year 2). Tests were performed on individuals (six controls, seven food-supplemented) that had nestlings in both years. Two control nests were excluded from the original data set because in the following year the nests failed before hatching, thus synchronization was not assessed. Change was calculated with the use of a paired t test (degrees of freedom = n − 1).

Year	Control (d)	Food-suppl. (d)	Difference (control vs. food-supp.)
1	5.17 ± 5.20	8.07 ± 4.69	t_{11} = −1.05
2	4.00 ± 3.21	11.36 ± 3.93	t_{11} = −3.65**
Change	t_5 = 0.63	t_6 = −2.63*	

*P < 0.05. **P < 0.005.

according to their past experience. A decision rule specifies the trait (laying date, in this case) as a function of an estimate of future environmental suitability made at the time of making the decision. Such a rule may be genetically determined, but birds might be expected to recalibrate this rule if it appears to produce a mismatch between breeding and the conditions for feeding the young (*17*, *18*) (in this case, a temporal mismatch between nestling phase and caterpillar peak date).

Learning when is best to breed is only adaptive when the environment in a certain locality carries some information on the environment at the time of the next breeding event. The shifts in laying date shown in this study may be viewed as a mechanism by which birds adapt their breeding time to the local environmental conditions. This is particularly relevant for species such as the blue tit that may settle in a wide variety of habitats, but once settled will breed at that same location for the duration of their lives. The seven localities on the Hoge Veluwe, for which we measured caterpillar biomass patterns for 1993 to 2000, differed in the peak date of caterpillar biomass (effect of locality on variation in local peak dates across 8 years: $F_{7,42} = 11.0, P < 0.0001$ corrected for year). This indicates that some sites are consistently earlier than others, independent of the between-year differences. If the best time for rearing the offspring (i.e., the caterpillar peak date) in a certain locality is consistently earlier or later than in other localities, birds are expected to benefit from learning.

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7. The study was carried out in the National Park De Hoge Veluwe, central Netherlands. The area consists of plots of mixed forest dominated by oak (*Quercus robur*) and Scots pine (*Pinus sylvestris*) and into which 400 nest boxes were placed. Nest boxes were checked daily from the end of March until early May during the breeding seasons of 1997 to 2000, so that the exact day on which the first egg was laid was known. Laying date is expressed in terms of April date, e.g., 1 = April 1st, 35 = May 5th.
8. Mealworms (*Tenebrio molitor*) and larvae of the waxmoth (*Galleria mellonella*) were placed in small trays inside the nest box from the day of hatching of the first egg to the day of fledging of the young in the breeding seasons 1997 to 1999. Feeding trays were placed near the entrance hole, so that only the adults could take the food. In the first 6 days after hatching, food consisted of a mixture of the two species, whereas afterward it was composed of mealworms only. The amount offered increased approximately linearly from 1.0 g/day on day 0 to 20 g/day on day 10 after hatching and then leveled off at 20 g/day for a 12-chick brood. Proportional adjustments in quantity were made for smaller and larger broods. Remaining food was replaced each day with the scheduled amount. Half of the nests were food-supplemented, whereas the other half served as a control. Treatments were chosen within pairs of nests with similar hatching dates. An effort was made to assign different treatment levels to nests in similar habitats.
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16. For each female that laid in 2 successive years we calculated (i) the difference in laying date between the 2 years (laying date$_{\text{year 2}}$ – laying date$_{\text{year 1}}$) and (ii) the between-year difference in the mean laying date of the females other than the 15 experimental ones (Fig. 1) laying in nest boxes, within a radius of 200 m from the focal nest box of the female (mean laying date$_{\text{year 2}}$ – mean laying date$_{\text{year 1}}$). This difference is an estimate of the change in the environment experienced by the focal females (*6*). On average, we used 2.8 ± 1.0 (SD) neighbor nests for each focal nest. Control and food-supplemented nests did not differ in the average laying date of neighbor nests (year 1, $F_{1,11} = 2.13$ and $P = 0.17$; year 2, $F_{1,11} = 1.64$ and $P = 0.23$, controlling for year). We calculated the regression of between-year difference in laying date on the difference in mean laying date of neighbors ($R^2 = 0.51$, $n = 15$; $F_{1,13} = 13.59$, $P = 0.003$), so that its residuals were the between-year changes in laying date of individual females independent of the neighbors. The degree of synchronization between tits' breeding and the caterpillars was defined as the difference in days between day 10 of the tits' nestling period (approximately the midpoint of the nestling period) and the caterpillar peak date. For this latter, we used the average of the study area because the seven sampling sites did not coincide with blue tit territories. Throughout the text, food-supplemented females refer to females receiving food in the nestling phase.
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Bile Acid Secreted by Male Sea Lamprey That Acts as a Sex Pheromone

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We show that reproductively mature male sea lampreys release a bile acid that acts as a potent sex pheromone, inducing preference and searching behavior in ovulated female lampreys. The secreted bile acid 7α,12α,24-trihydroxy-5α-cholan-3-one 24-sulfate was released in much higher amounts relative to known vertebrate steroid pheromones and may be secreted through the gills. Hence, the male of this fish species signals both its reproductive status and location to females by secreting a pheromone that can act over long distances.

The sea lamprey, *Petromyzon marinus*, is an ancestral jawless fish and an invasive parasite of fishes, particularly in the Laurentian Great Lakes of North America. It migrates into streams to spawn in the spring. The males arrive earlier than the females (*1*) and build nests in areas where flow rates are 0.5 to 1.5 m s^{-1} (*1*, *2*). It has long been suspected that the males release a pheromone to guide the females to their nests (*3*, *4*). This type of sex pheromone, capable of inducing spatial orientation of conspecifics "downwind," is well established in insects (*5*), but not so in vertebrates, whose identified sex pheromones tend to have a small

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