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Parent-Offspring Conflict and Coadaptation

Camilla A. Hinde, Rufus A. Johnstone, Rebecca M. Kilner

The evolution of family life has traditionally been studied in parallel by behavioral ecologists and quantitative geneticists. The former focus on parent-offspring conflict and whether parents or offspring control provisioning, whereas the latter concentrate on the coadaptation of parental supply and offspring demand. Here we show how prenatal effects on offspring begging can link the two different approaches. Using theoretical and experimental analyses, we show that when offspring control provisioning, prenatal effects primarily serve the parent's interests: Selection on parents drives coadaptation of parent and offspring traits. In contrast, when parents control provisioning, prenatal effects primarily serve the offspring's interests: Selection on the offspring drives coadaptation of parent and offspring traits. Parent-offspring conflict may thus be responsible for the selective forces that generate parent-offspring coadaptation.

The complex social interactions that underpin family life are of considerable interest to both behavioral ecologists (1–4) and quantitative geneticists (5–7). Yet researchers in each field have largely ignored the questions raised by the other (8). Behavioral ecologists have focused on the evolutionary conflict of interests between parents and their young (1, 2) and how it is resolved (9): Is it offspring who control provisioning or parents? Quantitative geneticists, in contrast, have focused on parent-offspring coadaptation: How is parental supply correlated with offspring demand, and is this correlation attributable chiefly to selection on parents or selection on offspring? We show here that both sets of questions are, in reality, tightly linked.

The empirical connection between the two approaches lies in the recent discovery that maternal substances in the developmental environment, such as testosterone, antibodies, and carotenoids, modulate later expression of offspring solicitation behaviors (10–12). In some cases, these maternal effects match offspring begging to parental capacity by providing a prenatal cue of parental generosity (13, 14), thus facilitating the coadaptation of offspring and parental behaviors (7, 8, 14). However, although it is commonly assumed that this arrangement favors the mother (10, 11, 15), it is in fact unclear whether maternal effects serve the evolutionary interests of parents or offspring (4, 13, 14). Here we show how understanding the role of maternal effects in resolving parent-offspring conflict can help to explain how and why a correlation arises between parental supply and offspring demand.

We begin with a theoretical analysis, in which we extend existing models of parent-offspring conflict resolution to incorporate variation in parental supply (attributable to variation in the cost of provisioning) and allow offspring to adjust their demand in response to prenatal cues of parental generosity. We then explore the predicted consequences of disrupting the correlation

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between parental supply and offspring demand by exchanging young between parents. We show that when offspring control provisioning, it is parents who are predicted to suffer most when young are exchanged; under these circumstances, maternal effects primarily serve the parent's interests, and it is selection on the parents that is responsible for the coadaptation of parent and offspring traits. In contrast, when parents control provisioning, it is offspring who are predicted to suffer most when young are exchanged; under these circumstances, maternal effects primarily serve the offspring's interests, and it is selection

on the offspring that drives coadaptation of parent and offspring traits.

We focus on provision of food by a parent to a brood (treating the brood as a single unit). The fitness benefit of provisioning to the offspring depends on the amount of food provided, y, and upon offspring need, n, and is denoted $b(n,y)$ [where $b(n,0) = 0$]. We assume that $\partial b/\partial y > 0$, $\partial^2 b/\partial y^2 < 0$, and $\partial^2 b/\partial y \partial n > 0$, implying that greater quantities of food yield greater benefits and that the marginal benefits of provisioning increase with need but decrease with quantity provided. Provisioning also entails a cost to the parent (it reduces future reproductive success), which depends on the amount of food provided and on parental quality, q, and is denoted $c(q,y)$ [where $c(q,0) = 0$]. We assume that $\partial c/\partial y > 0$, $\partial^2 c/\partial y^2 \geq 0$, and $\partial^2 c/\partial y \partial q < 0$, implying that provision of more food entails greater costs and that the marginal cost of provisioning is non-decreasing with quantity provided but decreases with the quality of the parent (we assume that $\partial b/\partial y > \partial c/\partial y$ for $y = 0$ and $n > n_{min}$, implying that parents stand to gain by supplying at least some food to offspring of greater than the lowest possible level of need n_{min}). For simplicity, we shall also assume that costs incurred by the parent do not affect the fitness of its mate.

Suppose that offspring are related to their parent's future progeny by a coefficient r (>0). Provided that $r < 1$, there exists a conflict of interest between parent and young over resource
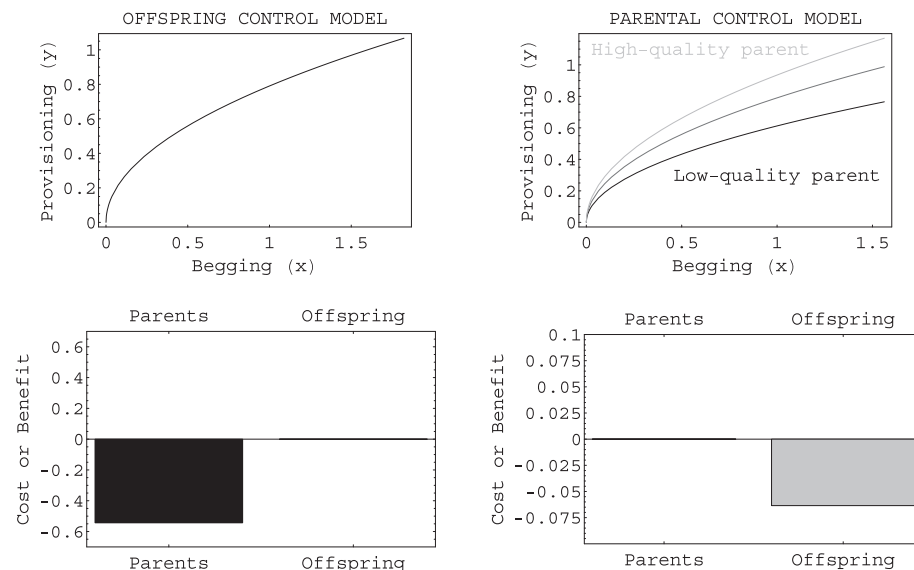

Fig. 1. Provisioning behavior and predicted consequences of exchanging young, under the offspring control and parental control models. All results are for the specific illustrative case in which $b(n,y) = ny - y^2/2$, $c(q,y) = 16y^2/(1 + 8q)$, $Y(x) = \sqrt{5x/8}$, parental quality is evenly distributed between 0 and 1, and offspring need is drawn from a scaled beta distribution ranging from 0 to 5. Upper graphs show provisioning as a function of offspring begging intensity under the offspring control and parental control models; in the latter case, successively lower curves correspond to parents of high, medium, and low quality ($q = 1/4$, $1/2$, and $3/4$). Lower graphs show the expected direct fitness impact of exchanging eggs on parents (black bars) and on offspring (gray bars) under both models; values are scaled relative to the standard deviation in expected direct fitness across parents of different qualities under normal conditions. There are different scales on the two lower graphs: The impact of egg exchange is much larger under the offspring control model.

allocation. Now let us contrast two models of conflict resolution. Under the offspring control model, offspring invest some level of effort x in costly begging in order to extract food from the parent. The parental response in this case is externally specified and cannot be adjusted optimally in relation to parental quality. Under the parental control model, parents may actively choose how much food to supply but benefit by attending to costly begging on the part of the offspring because this serves as a signal of condition.

In both models, offspring should be expected to adjust their begging effort in response to cues of maternal quality present in the egg (16). But what is the effect of swapping eggs between parents and thereby scrambling the cues of parental quality available to the offspring? The answer depends on whether the parents or offspring control resource allocation.

Consider two parents of quality q_1 and q_2 (we assume without loss of generality that $q_1 > q_2$), who produce offspring of need n_1 and n_2, independently drawn from a distribution with probability density $f(n)$. We wish to determine both the expected direct fitness costs incurred by these parents and the expected direct fitness benefits obtained by their offspring, under normal circumstances and when the offspring are exchanged (as eggs) between the parents. In the latter case, we assume that the offspring receive cues of parental quality corresponding to their original parent rather than the parent with whom they actually interact [i.e., experimental results described in (14)].

Under the offspring control model (regardless of the precise form of the various cost and benefit functions), exchanging young is predicted to have no net effect on the expected direct fitness of offspring, but a negative effect on the expected direct fitness of parents (Fig. 1). It is thus parents who normally benefit directly from the modulation of offspring behavior in response to cues in the egg. In contrast, under the parental control model (again regardless of the precise form of the various cost and benefit functions), exchanging young is predicted to have no net effect on the expected direct fitness of parents, but a negative effect on the expected direct fitness of offspring. Under normal circumstances, it is the offspring who benefit directly from the information provided by cues in the egg. In Fig. 1 we show these predicted results graphically for a specific illustrative case.

We tested these two contrasting predictions, using the domesticated canary *Serinus canaria* (16). Canaries are ideal for such work because we know from previous work that canary parents provide more food when nestlings beg more intensely (17, 18) but that unrewarded begging is costly because it can retard nestling growth (19). In addition, a prenatal cue that influences offspring begging behavior has been well characterized (14, 20–22). Mothers deposit small quantities of maternal androgens [and possibly other substances (11, 12)] in the egg (20), and the precise

dose varies among clutches according to maternal and environmental conditions (23), with downstream effects on nestling begging intensity (14, 22). Because canaries have been inbred for many gen-

erations to produce distinct types (24), any genetic variation in begging behavior within each type is likely to be relatively small (25). We therefore assume that much of the variation among canary
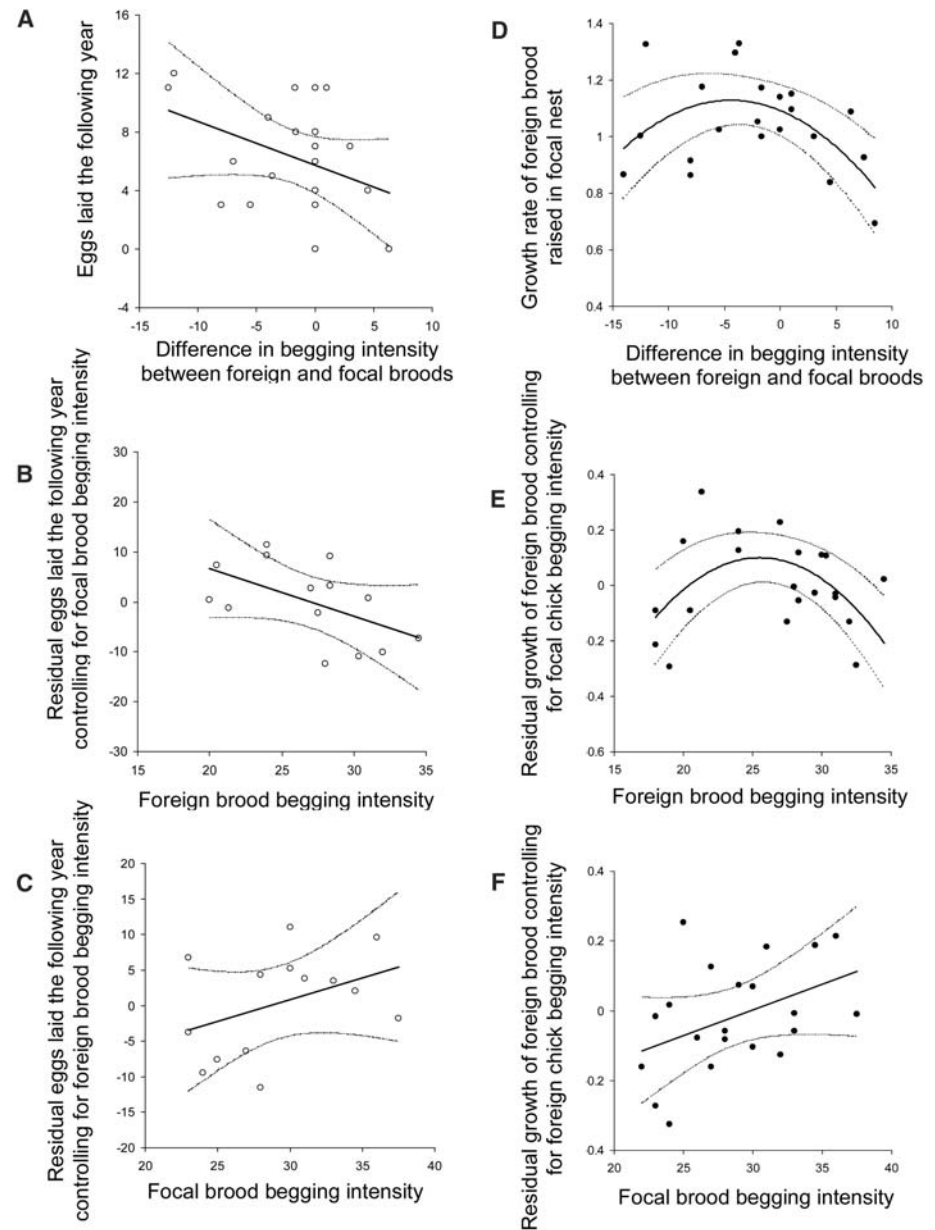

Fig. 2. Regression plots showing (**A**) the effect of a change in brood demand at the focal nest on maternal fecundity the following year. Each data point represents one mother ($n = 21$ females that reared one brood of their own and one foreign brood; $n = 8$ control females that reared two broods of their own). The least-squares regression line is shown with 95% confidence intervals (CIs). (**B**) The correlation between the mean begging intensity of the foreign young in the focal nest and the residuals of maternal fecundity the following year after controlling for focal chick begging intensity. (**C**) The correlation between the mean begging intensity of the focal young and the residuals of maternal fecundity the following year after controlling for foreign chick begging intensity. In (B) and (C), lines of fit with 95% CIs are shown. (**D**) The effect of a change in brood demands at the focal nest on the growth rate of the foreign brood. Each data point is collected from one pair ($n = 21$ pairs with begging data that reared one foreign brood and one brood of their own). (**E**) The correlation between the mean begging intensity of the foreign young in the focal nest and the residuals of the growth rate of the foreign brood after controlling for focal chick begging intensity. (**F**) The correlation between the mean begging intensity of the focal young and the residuals of the growth rate of the foreign brood after controlling for foreign chick begging intensity. In (E) and (F), the least-squares regression lines are shown with 95% CIs.

broods in nestling begging intensity (22) is attributable to maternal factors in the egg, an assumption further justified by the fact that our breeding females exhibited considerable variation in other aspects of prenatal investment such as egg mass and clutch size (16).

We began by determining whether parents or offspring control provisioning. To do this, we exploited our recent discovery that canary nestling begging intensity is strongly influenced by prenatal factors in the egg and is relatively unperturbed by a changed rearing environment (14). Cross-fostering broods between parents thus generates a long-term manipulation of brood begging intensity, and parents exposed to intensely begging broods should pay a fitness cost for supplying food at a greater rate. If offspring alone control the supply of food, then broods that beg most intensely should routinely receive the most food and exhibit the fastest growth rates. If parents have some control over provisioning, then parental quality, in conjunction with brood begging intensity, should influence how begging is rewarded. Highly demanding broods reared by low-quality parents should then suffer reduced growth rates when their costly begging is unrewarded.

In our experiment, parents were allowed to raise two broods per year: one of their own and one fostered from a different pair (16). For each breeding attempt, we measured brood begging intensity and the future fitness consequences of our manipulation for mothers and young (16). We quantified offspring fitness in our experiments by measuring their growth rate. Just as has been found in free-living passerines (26), the chance that our canary offspring survive until they are independent of their parents is strongly related to their rate of growth during the nestling period (Generalized Linear Mixed Effects Model: $F_{1,325.6} = 134.19$, $P < 0.001$, $n = 346$ chicks from 107 different pairs). Maternal future fitness was quantified by comparing the number of eggs that females laid the following year.

We found that provisioning was costly. Mothers that were exposed to a less demanding brood than their own laid more eggs the following year, whereas females that cared for a more demanding foster brood produced fewer eggs (simple linear regression: $R^2 = 0.25$, $F_{1,21} = 5.63$, $P = 0.019$; Fig. 2A). Using a multiple regression, we found

that the negative slope of this relationship was attributable to the demands of the fostered offspring ($R^2 = 0.33$, $t_{14} = -2.20$, $P = 0.048$; Fig. 2B) rather than to those of the mother's own brood ($t_{14} = 1.59$, $P = 0.14$; Fig. 2C).

We also found that parents mitigate the costs of provisioning by exerting a high level of control over the rate at which they provide food, as assumed by the parental control model. Although canary broods were able to use their begging behavior to enhance their growth rate, and hence gain fitness benefits, this was only possible within limits of generosity prescribed by parents (Fig. 2D). Foreign young raised in the focal nest grew at a faster rate if they begged more intensely, until their begging levels more or less matched the demands made by the focal brood (measured in a separate breeding attempt). Beyond this point, parents continued to feed begging young but presumably not sufficiently well to compensate for the high levels of energy expended during excessive begging (19), and so growth rates then fell (second-order polynomial regression: $R^2 = 0.30$, $F_{2,20} = 3.91$, $P = 0.022$; Fig. 2D). A multiple regression reveals the separate contribution of begging by foreign and focal broods to this curvilinear relationship. The begging of the foreign brood, mismatched with their foster parent's generosity (14), caused the curvilinear relationship shown in Fig. 2D [$R^2 = 0.33$, foreign brood begging $t_{20} = 2.40$, $P = 0.028$; (foreign brood begging)^2 $t_{20} = -2.43$, $P = 0.026$ (Fig. 2E)], whereas the begging of the focal brood was positively and linearly correlated with growth [focal brood begging $t_{20} = 2.26$, $P = 0.037$; (focal brood begging)^2 = NS, term dropped from minimal model (Fig. 2F)].

Having established that parents control provisioning in canaries, we next tested the parental control model's prediction that offspring should sustain the greater loss in fitness when exchanged between nests. Our second experiment mimicked our model by investigating how exchanging offspring between parents affected the mean fitness of parents versus offspring. Once again, parents were allowed to raise two broods per year: a brood of their own young and a brood of foster young from a different pair, each swapped before hatching (16).

Overall, we found that cross-fostered young grew at a slower rate on average than those that

were raised by their own parents [$F_{1,143} = 16.42$, $P < 0.001$; Fig. 3 (16)]. In contrast, mothers that had raised a foreign brood had similar mean fecundity the following year to that of mothers that had reared only their own offspring ($F_{1,36} = 0.014$, $P = 0.91$; Fig. 3). Just as predicted by the parental control model, offspring suffered a greater loss in direct fitness as a result of the disruption in prenatal signaling than did their mothers (General Linear Model: cross-fostering treatment × brood/mother, $F_{1,180} = 4.98$, $P = 0.027$) (16). Contrary to a widely held assumption (11), our data therefore show that the prenatal matching of offspring begging to parental capacity serves the offspring's evolutionary interests. Their mothers benefit only indirectly, through the effect on the young.

Our results also imply, as shown in Fig. 2D, that parental control of provisioning imposes stabilizing selection on the begging intensity of the brood (7). Within each family, nestlings optimally balance the costs and benefits of begging by matching their demands to parental quality (Fig. 2C, 2F) (14). This gives rise to the positive correlation between parental provisioning and nestling begging (6, 14, 27) predicted by quantitative genetic models when selection acts on offspring (7). However, it is probable that in some other species, provisioning at the nest is under the control of offspring rather than parents (3). Our theoretical analysis predicts that such offspring control would lead to selection on parents which, quantitative genetic models suggest, should give rise to a negative correlation between parental supply and offspring demand (7). In short, understanding who controls provisioning in the evolutionary conflict between parents and their young is key to understanding the selective pressures responsible for parent-offspring coadaptation. The challenge for future work is to identify the ecological factors that predict who controls the supply of parental investment and to determine their effect on the genes involved in parent-offspring interactions.

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Fig. 3. The average effect of cross-fostering on correlates of nestling and maternal fitness. White bars show the fitness correlates of the brood and the mother when the brood is reared by the natal mother; gray bars show the fitness correlates when it is cross-fostered. Means with standard error bars are shown.
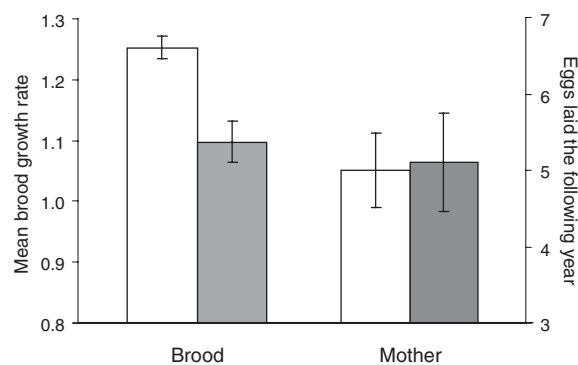
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Toward Extracting All Phylogenetic Information from Matrices of Evolutionary Distances

Sebastien Roch

The matrix of evolutionary distances is a model-based statistic, derived from molecular sequences, summarizing the pairwise phylogenetic relations between a collection of species. Phylogenetic tree reconstruction methods relying on this matrix are relatively fast and thus widely used in molecular systematics. However, because of their intrinsic reliance on summary statistics, distance-matrix methods are assumed to be less accurate than likelihood-based approaches. In this paper, pairwise sequence comparisons are shown to be more powerful than previously hypothesized. A statistical analysis of certain distance-based techniques indicates that their data requirement for large evolutionary trees essentially matches the conjectured performance of maximum likelihood methods—challenging the idea that summary statistics lead to suboptimal analyses. On the basis of a connection between ancestral state reconstruction and distance averaging, the critical role played by the covariances of the distance matrix is identified.

Information about evolutionary trees can be inferred from the fact that species that are close in the tree of life tend to have similar molecular sequences. In its most basic form, the evolutionary distance between two DNA sequences is estimated from the proportion of homologous sites differing between them, typically corrected for back-mutations under common modeling assumptions (*1*). For a collection of sequences, the pairwise evolutionary distances form a matrix—the distance matrix—which underlies a popular class of tree reconstruction methods. Technically, distance-matrix methods include all phylogenetic inference techniques relying solely on pairwise sequence comparisons, including neighbor-joining (NJ), BIONJ, WEIGHBOR, and FastME (*2–5*). Because of their simplicity, such methods are often considerably faster than parsimony- and likelihood-based approaches (*6, 7*), and distance-matrix methods are used for large-

scale phylogenetic reconstruction and bootstrap analysis or to produce starting trees for maximum likelihood (ML) heuristics. However, it is unknown if this advantage in speed affects accuracy adversely.

The use of distance-matrix information has been criticized for seemingly ignoring higher-order information, that is, data patterns involving more than two sequences (*1*). Moreover, it has been observed through combinatorial arguments that the conversion from molecular sequences to the distance matrix is far from invertible (*8*). However, this hypothesized information loss has not been quantified in a model-based framework. In reality, the comparison of distances between different pairs of sequences does involve higher-order signals, albeit in a highly summarized form. But it is unclear how to use such information. In particular, the correlation between the entries of the distance matrix has largely been ignored in the design and analysis of distance-matrix methods with a few notable exceptions (*3, 9, 10*).

Formally, phylogenetic data consist of *n* aligned DNA sequences of length *k* (without

gaps): $s_1^a,\ldots,s_k^a$, where *a* ranges over the *n* terminal taxa (Fig. 1). The evolutionary distance between the sequences at *a* and *b* is denoted by $\hat{\delta}(a,b)$. In the Jukes-Cantor model, a classical substitution model which treats all nucleotides symmetrically, the standard distance formula takes the form

$$\hat{\delta}(a,b) = -\frac{3}{4}\log\left(1 - \frac{4}{3}\ \hat{p}_{a,b}\right) \qquad (1)$$

where $\hat{p}_{a,b}$ is the proportion of homologous sites differing between sequences *a* and *b*.

A variety of distance-matrix methodologies have been proposed, of which this study focuses on agglomerative methods, including unweighted pair-group method using arithmetic averages (UPGMA) and NJ (*2, 11, 12*). Such methods proceed in two steps that are repeated until termination: (i) a selection step, where a pair of operational taxonomic units (OTUs) is selected for agglomeration, and (ii) a reduction step, where a reduced distance matrix is computed on the remaining OTUs. As an example, in the case of a molecular clock (that is, under the assumption that substitutions occur at the same rate in all branches of the tree), one can simply select the two closest

```
                1 23 45 67 8910
Homo sapiens    A-CAATGGAG-AAA
Pan             A-TAATA-AGCAAA
Gorilla         ATCA-CA-AGCGGA
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Fig. 1. Example of a DNA sequence data set. The alignment is typically obtained by using a multiple sequence alignment heuristic applied to the collected sequences. The dash is a gap. The columns are homologous sites; that is, they are derived from a common ancestor through substitutions. Those columns that include gaps are ignored. For instance, using the notation introduced in the text, we have *k* = 10, and the sequences at *a* = *Homo sapiens* and *b* = *Pan* are $s_i^a,\ldots,s_{10}^a$ = ACATGAGAAA and $s_i^b,\ldots,s_{10}^b$ = ATATAAGAAA, respectively. In particular, the preceding sequences agree on 8 out of 10 sites, so that $\hat{p}_{a,b}$ = 0.2 and $\hat{\delta}(a,b)$ = 0.457, using the Jukes-Cantor formula.

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