1   How basic components of information-updating interact to encourage variation in the results of

2   empirical studies of within and transgenerational plasticity

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Abstract

Experiences of parents and/or offspring are often assumed to affect the development of trait values in offspring because they provide information about the external environment, but it is currently unclear how information from different sources and times might combine to affect the information-states that provide the foundation for the patterns observed in empirical studies of developmental plasticity in response to environmental cues. We analyze Bayesian models designed to mimic fully-factorial experimental studies of within and transgenerational plasticity (TWP), in which parents, offspring, neither or both are exposed to cues from predators, to determine how different durations of cue exposure for parents and offspring, the devaluation of information from parents or the degradation of information from parents would affect offspring estimates of environmental states related to risk of predation at the end of such experiments. We show that the effects of different cue durations, the devaluation of information from parents, and the degradation of information from parents on offspring estimates are all expected to vary as a function of interactions with two other key parameters of information-based models of TWP: parental priors and the relative cue reliability in the different treatments. Our results suggest empiricists should expect to observe considerable variation across experimental studies of TWP based on simple principles of information-updating, without needing to invoke additional assumptions about costs, tradeoffs, development constraints, the fitness consequences of different trait values, or other factors.

Introduction

The trait values expressed by the offspring of one generation can be affected by their own experiences earlier in life (within-generational plasticity, WGP), by the experiences of their parents

35   (transgenerational plasticity, TGP), or by the combined effects of both (within and transgenerational

36   plasticity, TWP) [1-5]. It is often assumed that one reason why the experiences of parents and offspring

37   might have adaptive effects on offspring trait values is that those experiences provide information about

38   conditions in the external environment that the offspring are likely to experience later in life [6-12]. In

39   addition, information about conditions in the external environment can also be provided by genes,

40   inherited epigenic factors and parental phenotypes [7, 13, 14]. Hence, in order to appreciate how

41   information from an individual's distant and immediate ancestors and its own personal experiences

42   might combine to affect the development of traits that are the focus of studies of WGP, TGP or TWP, we

43   must consider how information from a variety of different sources combines within and across

44   generations to affect the information-state of that individual.

45   In principle, Bayesian updating is the best way to combine information from different sources

46   and different times to estimate the value of variables in the external environment [15]. As a result, in

47   recent years researchers have begun to use Bayesian approaches to study how information from

48   ancestors and personal experiences might combine over the course of ontogeny [16-22], review in [23].

49   These models assume that an individual's estimate of conditions in the external environment can

50   change over ontogeny, as its initial estimate based on information from its ancestors (its naïve prior

51   distribution) is updated on the basis of information provided by its own experiences. In turn, changes in

52   an individual's estimate over time are assumed to drive WGP, because an individual's estimate of

53   conditions in the external environment (e.g. its estimate of predator density at that locality) is assumed

54   to affect the trait values it develops in response to that estimate (e.g. its level of antipredator behavior).

55   By extension, these models predict that if different individuals with the same naïve prior distribution

56   were exposed to different informative experiences over the course of ontogeny, they would develop

57   different trait values in response to those experiences [16, 17, 20].

58   By definition, empirical studies of WGP, TGP and TWP focus on phenotypic traits, not

59   information-states. However, when WGP, TGP or TWP occur in response to cues that provide

60   information about the external environment, variation among individuals in their information-states

61   provides the foundation for variation in the trait values observed in experimental studies of these

62   phenomena. As a result, it is important to understand how the basic components of information-based

63   models (e.g. naïve priors, cue reliability, the duration of exposure to different cues, etc.) interact to

64   jointly affect the information-states of individuals. However, it is difficult to do this in information-based

65   models that generate predictions about the trait values of individuals. This is because such models

66   necessarily include assumptions about many factors in addition to an individual's information-state that

67   can affect the development and expression of its trait values (e.g. costs of sampling, developmental

68   constraints, or the fitness consequences of expressing different trait values)(ibid). As a result, in such

69   models, it is difficult to tell how much information-updating, per se, contributes to their results.

70   A different way to study how information-updating might affect developmental plasticity is to

71   focus on information-states, instead of phenotypes [19, 21, 22]. Models which consider how

72   information-states change within and vary across individuals as a function of variation in prior

73   distributions, cue reliability and other key components of information-based models have provided

74   insights into a number of topics in developmental biology, including the ways that information-updating

75   contributes to variation across individuals or genotypes in their developmental trajectories [19, 21, 24],

76   and to variation in age-dependent plasticity across individuals and among empirical studies [22]. These

77   analyzes indicate that empiricists can expect to observe a variety of different patterns in empirical

78   studies of these topics, simply based on the ways that we would expect information from different

79   sources to combine over ontogeny within individuals. By extension, these results suggest that it might

80   not be necessary to invoke assumptions about developmental constraints, tradeoffs, costs of sampling,

81   the fitness consequences of trait values, or other factors to account for at least some of variation in

82   results that empiricists have observed in studies of WGP.

83   Recently Stamps and Bell [25] extended this approach by using simple Bayesian approaches to

84   model experimental studies of TWP in response to informative cues. They found that interactions

85   between two basic components of such models (the parent's prior at the beginning of the study, and the

86   relative reliability of the cues in the different treatment groups) had profound effects on the patterns of

87   offspring information-states expected at the end of those experiments. Here, we expand these analyses

88   to consider three other variables that are likely to vary across experimental studies of TWP: 1)

89   differences between the duration of exposure to the same cues in parents and offspring, 2) the extent

90   to which information from parents is devalued, as compared to the information based on offspring

91   experience, and 3) the extent to which information from parents is degraded as it is passed from parents

92   to their offspring. As is described below, we consider how variation among experiments in these three

93   variables, in conjunction with variation among experiments in parental priors and the relative reliability

94   of the cues in the different treatments, would affect the patterns of offspring information-states

95   expected at the end of empirical studies of TWP.

96   As was the case in [25], we illustrate this approach by modelling fully-factorial experiments of

97   TWP in response to cues from predators, in which parents, offspring, both or neither are exposed to

98   cues from predators, and then the trait values of the offspring are measured at the end of the

99   experiment. Where P = exposed to cues from predators and N = not exposed to cues from predators,

100   and where the first letter indicates the parental treatment and the second letter indicates the offspring

101   treatment, the four treatment groups in this type of study consist of NN (neither parents and offspring

102   exposed to cues), PN (parent exposed, offspring not exposed), NP (parent not exposed, offspring

103   exposed) and PP (both parents and offspring exposed).

104   The results described in [25] were based on assumptions about experimental design and

105   information-updating which are unlikely to be valid in many empirical studies of TWP. First, with respect

106   to experimental design, we assumed that parents and offspring were exposed to the same cues for the

107   same period of time. This assumption is frequently violated in experimental studies of TWP. For

108   instance, of the 13 experimental studies of TWP in response to cues from predators listed in a recent

109   review [26], the duration of exposure to the cues for parents and for their offspring differed in 11 of

110   them. Hence, one important question is whether and how different durations of exposure to the same

111   cues in parents and offspring might contribute to differences among the offspring in TWP experiments

112   in their information states at the end of these experiments.

113   Second, in [25] we assumed that exposure to the same cues for the same period of time in

114   parents and offspring would provide the same information to offspring. There are at least two reasons

115   why this assumption need not be valid. First, theory indicates that information based on parental

116   experiences should be devalued, relative to information based on offspring experiences, if

117   environmental conditions might change across or within generations [7, 27]. In nature, changes between

118   generations in the value of a state of the environment can occur if offspring develop in a different

119   environment than their parents, e.g. as a result of natal dispersal in spatially heterogeneous

120   environments [11, 14] or as a result of temporal shifts in environmental conditions that may occur

121   between generations [7, 11]. The results of recent studies of experimental evolution in nematodes

122   support the hypothesis that temporal autocorrelation for the environments of parents and offspring

123   encourage the evolution of transgenerational plasticity, by showing that parental experiences had

124   adaptive effects on offspring traits in lineages which evolved when the environmental conditions during

125   the parental and offspring generation were strongly correlated with one another, but not in lineages in

126   which they were not [28, 29].

127   In addition, if environmental conditions might change within generations, a parent's estimates

128   of those conditions based on their experiences earlier in life might no longer be accurate by the time

129   that they transmit information about these conditions to their offspring [7, 30]. This possibility is

130   implicitly acknowledged by empiricists who study TWP when they use experimental protocols that

131   minimize the time that elapses between parental exposure to the cues and the time when parents

132   transfer information to their offspring (e.g. when parents are exposed to cues from predators as adults,

133   just before offspring production)[e.g. 31-32].

134   Second, information from parents might be degraded between the time that parents perceived

135   the cues and the time that parents transferred information based on those cues to their offspring.

136   Degradation of information from parents based on their exposure to a given cue is likely because the

137   transmission of information from parents to offspring requires additional proximate steps that are not

138   required when offspring are directly exposed to the same cue [30]. For instance, parents that detect a

139   cue from predators might produce a signal (e.g. alter their parental behavior) based on their updated

140   estimate of the chances that this predator lives nearby [34]. Then their offspring would need to detect

141   this signal and use it to update their own estimate of the probability that the predator is in residence.

142   Since neither the parent's production of the signal nor their offsprings' detection of that signal are likely

143   to be error-free, the information based on the parent's experience could become less reliable by the

144   time it reaches their offspring. In contrast to the devaluation of information provided by parents, which

145   is assumed to be an adaptive response to spatial and or temporal heterogeneity in environmental

146   conditions, the degradation of the information provided by the parents is assumed to be an unavoidable

147   consequence of the noise introduced into the information pathway by the proximate mechanisms by

148   which parents pass information based on their own experiences along to their offspring.

149   Hence, in the current study we considered how differences in the duration of exposure to the

150   same cues in parents and offspring and the devaluation or degradation of information from parents

151   would interact with previously-examined variables (parental priors, relative cue reliability) to affect the

152   patterns of offspring estimates expected at the end of the treatments in experimental studies of TWP in

153   response to cues from predators.

154

Material and methods

156   Details about the design and biological rationale for the models used as the basis for those in

157   the current article are provided in previous publications [19, 21, 22, 25]. In brief, we assumed that each

158   parent began with a prior distribution (Prior), based on information from their ancestors (e.g. via genes,

159   inherited epigenetic factors, grand-parental experiences), as well as any informative experiences the

160   parents had before the onset of the experiment. We illustrate the results for three informative parental

161   Prior distributions, with different means (0.1, 0.5 and 0.9), but the same variance (0.04) (For definitions

162   of these and other terms, see Supporting Information).

163   We assumed that cues from the predator in the P treatment were always informative, and used

164   beta functions with shapes modelled by $\alpha > \beta$ to indicate the shapes of the cumulative likelihood

165   functions for the conditions in the P treatments. We analyzed two sets of models which differed with

166   respect to their assumptions about the reliability of the information provided by the N treatment. In the

167   first set (N- models), the information provided by the N treatment was less reliable than the information

168   provided by the P treatment. We analyzed this situation by assuming that the information provided by

169   conditions in the P treatment was highly reliable (likelihood with a shape modelled by $\alpha = 8$, $\beta = 1$) while

170   conditions in N provided no information about the state (i.e., the cumulative likelihood function for the

171   N treatment had a uniform distribution ($\alpha = 1$, $\beta = 1$). In the second set of models (N* models), the

172   information provided by the P treatment and the information provided by the N treatment were equally

173   reliable. In this case, the cumulative likelihood function for the N treatment was the mirror-image of the

174   cumulative likelihood function for the P treatment. For instance, if the experiences in the P treatment

175   resulted in a cumulative likelihood function that indicated with a high level of reliability that the value of

176   the state of the environment was likely to be high (e.g. likelihood modelled by a beta distribution with a

177   shape indicated by $\alpha = 8$, $\beta = 1$), conditions in the N treatment had a cumulative likelihood function that

178   indicated with the same level of reliability that the value of the state was likely to be low (e.g. likelihood

179   with a shape modelled by $\alpha = 1$, $\beta = 8$).

180   For all of the models, we computed the offspring estimates of the value of the state at the end

181   of their respective treatments, where each estimate was the mean of the offspring posterior distribution

182   at the end of the experiment. Hence, in the current article, 'offspring estimate' indicates a key

183   component of the offspring's information-state at the end of the experiment, namely, its best estimate

184   of the value of the state of the environment at that point in time.

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186

Duration of exposure to the same cue in parents and offspring

188   Preliminary analyses showed that if parents and offspring were exposed to the same cues for

189   the same period of time, differences between the parental and the offspring generation in the age of

190   onset of the exposure period had no effects on the results. For instance, our analyses indicated that

191   offspring estimates of predator density would be the same if their parents had been exposed for two

192   weeks to cues from predators just before gamete production as if the offspring themselves had been

193   exposed for two weeks to the same cues as juveniles. These results occur because in Bayesian updating

194   models which assume that the true state of the environment is unlikely to change over time, if different

195   subjects with the same prior distribution are exposed to the same cues, the order in which they were

196   exposed to those cues has no effect on their final posterior distributions. Because the order-indifference

197   of Bayesian updating is particularly relevant to analyses of sensitive periods and age-dependent

198   plasticity, we defer discussion of this point to a study of that topic (Stamps, in prep.)

199   In contrast, preliminary analyses suggested that different durations of exposure to the same

200   cues in parents and offspring might have strong effects on offspring estimates at the end of their

201   respective treatment periods. In order to investigate the effects of different durations of exposure to

202   the conditions P or N for parents and offspring on the results, we divided the total treatment period, T,

203   for each generation into four intervals of equal length, and then specified the likelihood function for

204   exposure to the cue for one interval, and the likelihood function for no exposure to the cue for one

205   interval. For instance, to model a situation in which parents were exposed to the cues for a longer

206   period than the offspring, we assumed that parents in the P treatment were exposed to cues from the

207   predator for all four intervals, whereas the offspring in the P treatment were exposed to the cues from

208   the predator for either one, two or three intervals, and were exposed to no cues from predators for the

209   remaining interval(s). Similarly, to model a situation in which offspring were exposed to the cues for a

210   longer period than the parents, we assumed that offspring in the P treatment were exposed to the cues

211   for all four intervals, but parents in the P treatment were exposed to the cues for one, two or three

212   intervals, and were exposed to no cues for the remaining intervals. In all of these models, the N group

213   was maintained with no cues from predators for all four intervals. We then used Bayesian updating to

214   compute the mean values of the offspring posterior distributions at the end of the offspring treatment

215   period for each of the treatment groups (NN, PN, NP and PP), based on the likelihood functions for the

216   four intervals in the parental generation and the four intervals in the offspring generation.

217   As in [25], we computed separate models for the N- situation (in which the conditions during

218   one time interval in the P treatment provided much more reliable information than the conditions

219   during one interval in the N treatment) and for the N* situation (conditions during one interval in the P

220   treatment provided information as reliable as the conditions during one interval in the N treatment).

221   For the N- models, we assumed that in a P treatment in which the individual was not exposed to the

222   cues in all four intervals, no information was provided in an interval that lacked the cue. That is, the

223   likelihood function for one interval spent in the absence of the cue had a shape indicated by a uniform

224   distribution (α =1, β = 1). In the N* models, we assumed that in a P treatment in which the individual

225   was not exposed to the cues in all four intervals, the information provided by one interval spent in the

226   absence of the cue was as reliable as the information provided by one interval spent in the presence of

227   that cue. For instance, if the likelihood function for one interval in the presence of cues from a predator

228   had a shape indicated by α = 2.5, β = 1, the likelihood function for one interval in the absence of those

229   cues had a shape indicated by α =1, β = 2.5.

230

Cues based on parental experience are devalued or degraded

232   Although the devaluation and the degradation of information from parental experiences are

233   assumed to occur as a result of different processes (see Introduction and Discussion), in both situations

234   it is assumed that the information provided by the signal that parents pass along to their offspring based

235   on their exposure to a given cue is less reliable than the information provided by the cue to which the

236   parents had been exposed. In Bayesian terms, this means that although we would expect the likelihood

237   function for the signal provided to their offspring by parents in the P treatment to have the same mean

238   value as the cue in the P treatment for the offspring, we would expect the likelihood function for the

239   parental signal to have a higher variance than the likelihood function for the cues in the P treatment for

240   the offspring. Hence, we used the same procedure to model the devaluation of information from the

241   parents and the degradation of information from the parents. That is, we assumed for both situations

242   that the signal from the parent and the cue for the offspring had likelihood functions with the same

243   mean, but different variances. For instance, instance, if the likelihood function for the P treatment for

244   offspring had a shape modelled by $\alpha = 8$, $\beta = 1$ (mean = 0.89, variance = 0.01), the likelihood function for

245   the signal provided by parents to offspring by the parents in the P treatment might have a shape

246   modelled by $\alpha = 3.5$, $\beta = 0.44$ (mean = 0.89, variance = 0.02). That is, we assumed that exposure to cues

247   from predators in the P treatment yielded the same point estimate of the value of the state of the

248   environment for parents and offspring (in this case, a relatively high value of 0.89, on a scale of 0 to 1),

249   but the reliability of the information provided by the parents to their offspring (indicated by the variance

250   of the likelihood function) was lower than the reliability of the information provided by the same

251   experience for the offspring.

252   In the N- models, the reliability of the information for the P treatments differed for parents and

253   offspring, as was indicated above. However, given our assumption for these models that the information

254   in the N treatments was unreliable (see above), we assumed that the information provided by the N

255   treatments was equally unreliable for both the parent and the offspring generation (modelled by $\alpha = 1$,

256    $\beta = 1$).

257   In the N* models, in which conditions in the N treatment provided information as reliable as

258   those in the P treatments, we devalued the information provided by parents in the N treatment groups

259   to their offspring. For instance, if the likelihood function for the P treatment for the offspring had a

260   shape modelled by $\alpha = 8$, $\beta = 1$, the likelihood function for conditions in the N treatment for offspring

261   had a shape modelled by $\alpha = 1$, $\beta = 8$, but the likelihood function for the information provided by

262   parents to their offspring had a shape modelled by $\alpha = 0.44$, $\beta = 3.5$.

263   All of the other assumptions and parameter values for these models were the same as those for

264   the models described in [25].

265

266

Results

268   In the 'baseline' models, in which parents and offspring were exposed to the same cues for the

269   same period of time, and in which information from parents was neither devalued or degraded, the

270   resulting patterns of offspring estimates varied as a function of the relative reliability of the cues in the

271   different treatments and the parental Priors (Fig 1). In the N- models, in which the information provided

272   by conditions in one treatment (here P, indicating the presence of cues from predators) was much more

273   reliable than the information provided by the conditions in the other treatment (here, N, indicating the

274   absence of cues from predators), we observed a 'jump-up' pattern, in which the value for the NN group

275   was low, and the values for the other three groups (NP, PN, PP) were high and similar (but not identical)

276   to each other. However, this pattern only occurred when the state of the environment indicated by the

277   parental Prior differed from the state indicated by the cue in the P treatment. Since we assumed here

278   that the cues in the P treatment indicated that the value of the state of the environment was high, we

279   observed the jump-up pattern when the parental Prior strongly contradicted the cue (Prior mean =

280   0.1)(Fig 1a). In contrast, when the parental Prior and the cues in the P treatment indicated the same

281   value of the state (Prior mean = 0.9), the offspring estimates were similar for all four treatment groups.

282   This result occurred because in these models, the N treatment had no effect on an individual's

283   information-state, so the results were primarily affected by the 'discrepancy rule' of Bayesian updating

284   (see [24] for more on this topic).

285   In the N* models, in which the information provided by conditions in the P treatment and the

286   information provided by conditions in the N treatment were equally reliable, we observed a 'step-up'

287   pattern, in which the offspring estimates for the NN treatment were low, those for the PP treatment

288   were high, and those for the NP and PN treatments were intermediate. In this case the pattern did not

289   vary as a function of the parental Prior: for the same set of parameter values, the step-up patterns were

290   similar for a range of parental Priors (Fig 1b). This result occurred because in the N* models, by the end

291   of the experiment reliable information about the state of the environment had been provided by the

292   cues in both treatment groups, so after the offspring were exposed to two doses of informative cues

293   (based upon the parent's experience and their own personal experience), the initial estimate provided

294   by the parental Prior no longer had much effect on their estimates of the value of the state of the

295   environment. These results have been described and discussed in detail in [25], so we merely present

296   examples of these patterns here for comparison with the results of the models in which we relaxed our

297   assumptions about cue durations, devaluation and degradation.

298

299   **Fig 1. How differences in the reliability of the cues in the different treatments affect offspring**

300   **estimates of the value of conditions in the external environment**. P treatment = exposure to cues from

301   a predator, N treatment = no cues from predator, first letter = parental treatment, second letter =

302   offspring treatment. Predicted offspring estimates at the end of an experiment for each of four

303   treatment groups (NN, PN, NP and PP) are indicated for parental Priors with three different means (0.1,

304   0.5, 0.9) and the same variance (0.04).   a. N- models: conditions in the N treatment provide much less

305   reliable information than conditions in the P treatment. In this example, information provided by

306   conditions in the P treatment is modelled by a cumulative likelihood function with a shape indicated by

307    $\alpha = 8$, $\beta = 1$, indicating that the value of the state is likely to be high; information provided by conditions

308   in the N treatment is modelled by a uniform distribution ($\alpha = 1$, $\beta = 1$).   b. N* models. Conditions in the

309   N treatment provide information as reliable as conditions in the P treatment; the likelihood functions for

310   the P and N treatments are mirror-images of one another. In this example, conditions in the P treatment

311   indicate with a high level of reliability that the state of the environment is likely to be high (likelihood

312   modelled by α = 8, β = 1); conditions in the N treatment indicates with equally high reliability that the

313   state of the environment is likely to be low (likelihood modelled by α =1, β = 8).

314   When parents and offspring were exposed to the same cues for different periods of time, the

315   main effect was to generate differences between the offspring estimates for the PN and NP groups;

316   these differences were not observed in the baseline models (compare Fig 1 with Figs 2 and 3). As

317   intuition would suggest, the offspring estimates were higher for the treatment group which included the

318   generation that had been exposed to the cues for a longer time. For instance, if the offspring in the P

319   treatment group were exposed to the cues for a longer period than their parents, PN < NP (Fig 2a,b).

320   Conversely, if the offspring in the P treatment group were exposed to the cues for a shorter time than

321   their parents, then PN > NP (Fig 3a,b).

322

323   **Fig 2. Duration of exposure to the same cues is longer for offspring than for parents**. In the P

324   treatment groups, parents are exposed to the presence of cues from predators for two of four time

325   intervals, but offspring are exposed to cues from predators for all four time intervals (see text).   a. N-

326   models. In this example, the likelihood function for exposure to cues from a predator for one time

327   interval has a shape indicated by α = 2.5, β = 1; the likelihood function for the absence of cues for one

328   interval has a shape indicated by a uniform distribution (α =1, β = 1).   b. N* models. In this example, the

329   likelihood function for exposure to cues from a predator for one interval has a shape indicated by α =

330   2.5, β = 1; the likelihood function for the absence of cues for one interval has a shape indicated by α =1,

331   β = 2.5.

332

333   **Fig 3. Duration of exposure to the same cues is longer for parents than for offspring**. In the P treatment

334   groups, parents are exposed to the presence of cues from predators for time four intervals, but offspring

335   are exposed to cues from predators for only two of the four time intervals (see text). Other variables are

336   the same as in Figure 2.

337

338   The overall patterns were otherwise similar to those found in the baseline models. That is, a

339   jump-up pattern was detectable in the N- models when the parental Prior indicated a different value of

340   the state than the cues in the P treatment, but not when the parental Prior indicated a value of the state

341   similar to the value indicated by the cues in the P treatment (Figs 2a, 3a). Similarly, similar step-up

342   patterns were detectable across a range of parental Priors in the N* models (Figs 2b, 3b). However, for

343   comparable sets of parameter values (i.e. for the same parental Prior, and for the same likelihood

344   function for the cues in the P treatment), the differences between the offspring estimates for the NP

345   and PN groups were much less pronounced for the N- models than for the N* models (compare Fig 2a

346   versus 2b, and Fig 3a versus 3b).

347   When information from the parents was devalued or degraded, the models predicted lower

348   estimates of the value of the state for the PN group than for the NP group (Fig 4). The overall patterns

349   were otherwise similar to those in the baseline models. A jump-up pattern was detectable in the N-

350   models when the parental Prior indicated a different value of the state of the environment than did the

351   cues in the P treatment, but not when the parental Prior indicated a value similar to that indicated by

352   the cues in the P treatment (Fig 4a). In addition, similar step-up patterns were detectable for all parental

353   Priors in the N* models (Fig 4b). However, for comparable sets of parameter values, the differences

354   between the offspring estimates for PN and NP were much less pronounced for the N- models (Fig 4a)

355   than for the N* models (Fig 4b).

356

357   **Fig 4. Information from parents is devalued or degraded before being passed to the offspring**. We

358   assume that parents and offspring in the P groups are exposed to the same cue for the same period of

359   time, with a likelihood function indicated by $\alpha = 8$, $\beta = 1$. However, the signal provided by the parent to

360   the offspring as a result of the parent's exposure to the cue is less reliable; it is modelled by a likelihood

361   indicated by $\alpha = 3.5$, $\beta = 0.44$.   a. N- model: information provided by conditions in the N treatment is

362   much less reliable than the information provided by conditions in the P treatment (likelihood for

363   conditions in the N treatment modelled by $\alpha = 1$, $\beta = 1$).   b. N* model: conditions in the N treatment

364   provide information that is as reliable as conditions in the P treatment (likelihood for N modelled by $\alpha =$

365   1, $\beta = 8$). However, the signal that parents provide to their offspring as a result of exposure to

366   conditions in the N treatment is less reliable, with a likelihood modelled by $\alpha = 0.44$, $\beta = 3.5$.

367

368   # Discussion

369   The current study suggests that empiricists should not be surprised to observe considerable

370   variation among experiments in the results of studies of trans and within generational plasticity (TWP) in

371   response to informative cues. Our results show that the offspring estimates that are assumed to provide

372   the foundation for the offspring trait values in such experiments are expected to vary as a function of

373   many factors, including 1) parental Prior distributions, 2) the relative reliability of the information

374   provided in the different treatments, 3) differences in the duration of exposure to the same cues for

375   parents and offspring, 4) the extent to which information based on cue-exposure for parents is

376   devalued, relative to the information based on cue-exposure for offspring, and 5) the extent to which

377   information passed from parents to offspring is degraded, relative to the information based on the

378   personal experience of the offspring. We illustrate these findings by modelling fully factorial

379   experiments in which parents, offspring, both or neither are exposed to cues from predators (in P

380   treatments) or are not exposed to those cues (N treatments).

381   Our results confirm previous results showing that interactions between parental Priors and

382   relative cue reliability are expected to have a major impact on the patterns of offspring information

383   states in empirical studies of TWP [25]. We analyzed two extreme situations for differences in the

384   reliabilities for the two treatments: N- models, in which the information provided by conditions in the N

385   treatment is much less reliable than the information provided by conditions in the P treatment, and N*

386   models, in which the information provided by the conditions in the P and the N treatments is equally

387   reliable. A possible example of the former might be an experiment in which the cues from the predator

388   in the P treatment consists of a single, near-escape from a predator over a period of several months. In

389   this case, conditions in the P treatment might provide a reliable indication that the predator in question

390   lives at the current locality, whereas the conditions in the N treatment may provide a less reliable

391   indication that it may not. By way of analogy, being the victim of a robbery once over the course of a

392   year might indicate with a high degree of reliability that thieves are active in your neighborhood, but if

393   such incidents rarely occur, not being robbed over the course of a year need not indicate with the same

394   level of reliability that they are not. An example of a situation in which the conditions in the P and the N

395   treatments might provide equally reliable information is when the subjects in the P treatment are

396   exposed for an extended period to a high concentration of kairomones from a predator and the subjects

397   in the N treatment are maintained in the absence of kairomones for the same period of time. In this

398   situation, investigators typically assume that the conditions in the P treatment reliably indicate that

399   predator density is high, whereas the conditions in the N treatment indicate with a comparable level of

400   reliability that predator density is low, since the concentration of kairomones never exceeded the preys'

401   threshold for detection (see [25] for additional discussion).

402   The current results confirm previous results indicating interactions between parental Priors and

403   the relative reliability of the cues in the different treatments (here P vs N) are expected to have major

404   effects on the patterns of offspring estimates in studies of TWP in response to informative cues. In

405   particular, the predicted patterns of offspring estimates were highly dependent on parental Priors in the

406   N- models, but virtually independent of parental Priors in the N* models [25].

407   These results imply that if investigators use an experimental protocol in which the information

408   provided by the different treatments differs in its reliability (as in the N- models), the results of their

409   experiments might vary as a function of the population-of-origin or the genotypes of their subjects. This

410   follows from the assumption that subjects from different populations might have different parental

411   Priors, based on information from their ancestors, e.g. from genes, inherited epigenetic factors or grand-

412   parental effects. In addition, if the parents for an experimental study of TWP were collected from the

413   wild, then variation among populations in parental experiences earlier in life could also contribute to

414   variation among populations in parental Priors. Along the same lines, different genotypes from the same

415   population might begin with different prior estimates of the value of the same state of the environment

416   [e.g. 24], so that the results of studies of TWP based on clonal organisms might vary depending on the

417   clone that was selected for the study.

418   Indeed, if investigators used an experimental protocol in which the conditions in the different

419   treatments differed with respect to the reliability of their information (as in the N- models), the choice

420   of population or genotype for a study might determine whether one could even detect plasticity. For

421   instance, in all of the N- models analyzed in this article, a 'jump-up' pattern (NN < PN,NP < PP) for

422   offspring estimates was observed when the value of the state of the environment indicated by the

423   parental Prior strongly contradicted the value of the state indicated by the cues in the P treatment.

424   However, when the value of the state indicated by the parental Prior was similar to the value indicated

425   by the cues in the P treatment, the offspring estimates were virtually identical in all four treatment

426   groups (NN≈ PN≈ NP≈ PP). In the latter situation, one would not expect to observe either WGP or TGP.

427   In contrast, consider a situation in which an investigator used an experimental protocol in which

428   the cues in the different treatments were all equally reliable (as in the N* models). In this case, our

429   results suggest that the choice of a population or a genotype for the experiment might not matter. As

430   we show here for all of the models, in this situation we expect to observe a similar step-up pattern (NN

431   < PN,NP < PP) regardless of the parental Prior.

432   As intuition would suggest, the main effect of assuming that cue duration differed for parents

433   and offspring or that the information provided by parents was either devalued or degraded was to

434   generate different values of the offspring estimate for the PN and the NP treatments; in the absence of

435   these assumptions, the offspring estimates were the same for the PN and NP treatments. However, for

436   the same parental Prior and for the same cues in the P treatment, the effects of differences in cue

437   duration or the devaluation or degradation of information from parents were much more pronounced in

438   the N* models than in the N- models. This suggests that in general, it would be easier to detect the

439   effects of cue duration or of the parental devaluation/degradation of information on offspring estimates

440   or trait values in TWP studies if one used an experimental protocol in which the information provided by

441   both treatments was similarly reliable than if one used a protocol in which the information provided by

442   one treatment was much more reliable than the information provided by the other.

443   If we just focus on situations in which the information provided by the conditions in both

444   treatments is equally reliable (the N* models), the results indicate, as intuition would suggest, that the

445   effects of those exposures on offspring estimates would be stronger for the generation that was

446   exposed to the cues for the longer period of time. This result supports earlier suggestions that under

447   natural conditions, parental experiences might have a stronger impact than offspring experiences on the

448   phenotypes of offspring during the juvenile period, because the cumulative experiences of parents over

449   their lifetimes provides more reliable information than is provided to offspring based on their own

450   experiences since conception [35, 36]. As a practical matter, these results indicate that variation among

451   experimental studies of TWP in the relative duration of exposure to the same cues for parents and

452   offspring would, all else being equal, be expected to contribute to variation in their results.

453   The models of information-updating presented here may also provide a useful point of

454   departure for investigating other aspects of the timing of cue-exposure that might contribute to the

455   variation results observed in empirical studies of TWP. For instance, the models analyzed herein ignore

456   sensitive periods, i.e. situations in which exposure to the same cues have different effects on trait

457   values, depending on the age of onset of the cue-exposures [37-40]. Although traditionally the literature

458   on sensitive periods has focused on the effects of an individual's own experiences early in life on its trait

459   values later in life (i.e. WGP), recently researchers have begun to consider the possibility of sensitive

460   periods for TGP, i.e. situations in which exposure to cues for parents have different effects on the trait

461   values of their offspring, depending on the age at which those exposures occurred in the parents, or the

462   age at which the offspring received the information from their parents [e.g. 26, 30, 41]. However, at this

463   point it is unclear how sensitive periods of parents, offspring or both would interact to affect offspring

464   estimates of conditions in the external environment.

465   As a general rule, we would expect the effects of sensitive periods on offspring information-

466   states to depend on the protocol used in a given experiment. Personal exposure to cues in the external

467   environment can't begin to affect the information-states of offspring until the offspring have become

468   capable of detecting those cues (e.g. as embryos, newborns, or hatchlings). An additional complication is

469   that in order to demonstrate that cue-exposure for parents affects the trait values of their offspring,

470   exposure to cues in the external environment for parents must end before their offspring become

471   capable of detecting the cues on their own. Hence, if both parents and offspring were continuously or

472   repeatedly exposed to the cues of interest from the embryo stage until just prior to offspring

473   production, both generations would be exposed to those cues throughout their sensitive periods, no

474   matter if or when they occurred in either generation. In that case, the predicted patterns of offspring

475   estimates would be the same as those predicted in the absence of sensitive periods (e.g. see Figs 1 and

476   4). However, if parents or offspring had sensitive periods for the effects on cue-exposures on offspring

477   trait values, if these periods occurred at different ages in the two generations, and if exposure to the

478   inductive cues was limited to restricted periods in both generations, then the effects of sensitive periods

479   on offspring estimates are unclear. This would be a worthwhile topic for further empirical and

480   theoretical study.

481   Our results also confirm the intuitive notion that when information from parents is devalued

482   relative to information from offspring, exposure to cues for parents would have a weaker effect on

483   offspring estimates than equivalent exposure to the same cues in the offspring. Theory predicts that the

484   devaluation of information from parents should occur as an evolved, adaptive response to reduced

485   levels of autocorrelation between parental environments and offspring environments (see Introduction).

486   In other words, the devaluation of information from parents is expected when, under natural conditions,

487   the value of a state of the environment is likely to change between the time that parents are exposed to

488   cues and the time that their offspring are exposed to the same cues. For instance, if we assume that the

489   true value of the state gradually changes over time, the devaluation of information from parents would

490   be inversely related to the amount of time that elapsed between the time that parents were exposed to

491   cues and the time that their offspring were exposed to the same cues. In turn, this implies that for

492   subjects from the same population, the devaluation of information from parents would be less

493   pronounced in an experiment in which parents were exposed to the cues of interest just before their

494   offspring were conceived and their offspring were exposed to the same cues soon after hatching than in

495   an experiment in which both parents and offspring were exposed to the cues soon after hatching.

496   Of course, in natural populations, the true value of a state of the environment need not change

497   gradually over time, but may instead occur at specific times, lifestages or life-history landmarks. For

498   instance, in a species in which the value of a state (e.g. predator density) does not change over the

499   distances typically traveled by natal dispersers, information based on a parent's exposure to kairomones

500   from a predator in its natal habitat would be also be relevant to its offspring's estimate of predator

501   density in its own natal habitat. In contrast, in a species in which predator density varies over typical

502   dispersal distances, information based on a parent's exposure to kairomones in its natal habitat would

503   be less useful for estimating the predator density in its offspring's natal habitat. In other words, theory

504   suggests that we should expect the devaluation of information from parents to differ among different

505   populations or species, depending on the extent to which the environmental factors of interest varied

506   spatially over the distances relevant to natal dispersal, or varied temporally within and across

507   generations. Hence, one could potentially test predictions about the devaluation of information from

508   parents using comparative data from field studies indicating whether, how, and when particular

509   environment conditions of interest are spatially and temporally correlated for parents and their

510   offspring. Unfortunately, at present this data is still sparse [42-44].

511   In addition, our results also indicate that if information from parents is degraded before it is

512   passed along to their offspring, exposure to cues for parents would have a weaker effect on offspring

513   estimates than equivalent exposure to the same cues in offspring. However, in contrast to the duration

514   of exposure to cues, which can be readily manipulated or controlled by investigators, the degradation of

515   information from parents cannot. The degradation of information from parents is assumed to occur as a

516   non-adaptive consequence of the proximal mechanisms by which parents transfer information to their

517   offspring. That is, the degradation of information from parents to their offspring is assumed to be a

518   result of the 'noise' introduced into the flow of information from one generation to the next, based on

519   the series of processes that intervene between the time that mothers and/or fathers are personally

520   exposed to the cues and the time that an offspring receives signals from their parents based on the

521   parent's estimate of the value of the state [30].

522   Because we assume that the degradation of information occurs as a result of unavoidable

523   constraints in the mechanisms responsible for the transfer of information across generations, we would

524   expect the degradation of information from parents to be phylogenetically conservative, i.e. similar for

525   populations and species with comparable patterns of offspring development and parental care. Thus, in

526   contrast to the situation for the devaluation of information from parents, we would not expect the

527   degradation of information from parents to vary across populations or closely-related species, as a

528   function of the extent to which the environmental conditions experienced by parents and offspring were

529   correlated with one another across space and time. Instead, testing hypotheses about the effects of the

530   degradation of information from parents to offspring will require detailed information about the

531   proximal mechanisms which mediate the flow of information from parents to offspring in a given taxon.

532   At present, little is known about this topic; this would be another fruitful topic for future research.

533   Under certain conditions, models which predict patterns of offspring estimates may help shed

534   light on the patterns of offspring trait values observed in empirical studies of TWP. One important

535   condition is that the inductive cues only provide information, as opposed to also having direct, long-

536   lasting effects on the somatic states of parents, offspring or both. Detailed discussion of the difference

537   between inductive experiences which affect development because they provide information and

538   inductive experiences which affect development because they have persistent effects on somatic states

539   can be found in [6, 9, 45, 46]. Examples of information-only inductive experiences include stimuli

540   produced by predators, conspecifics, or competitors. Examples of inductive experiences which might

541   provide information, but which also have direct effects on a developing organism's somatic state,

542   include food deprivation in animals, shade in plants, and extreme temperatures in either. As Nettle and

543   Bateson (2015) point out, if an inductive experience is information-only, one can imagine a single loss-

544   of-function mutation that abolishes an individual's ability to detect that cue, but which leaves the

545   developing individual otherwise unaffected. In contrast, if an inductive experience has a direct and

546   lasting impact on an individual's state, one would expect that experience to affect its trait values even if

547   the individual was unable to sense that it had that experience. Although it is possible to make general

548   predictions about how particular trait values might change in response to exposure to information-only

549   cues over the course of development [e.g. 17, 20], this is much more difficult when experiences also

550   have direct, lasting effects on an individual's metabolism, growth or other aspects of its somatic state

551   (but see 16).

552   A second important condition for assuming that offspring estimates will be directly related to

553   the expression of a given trait in the offspring is evidence that the trait is advantageous when the

554   offspring is in the environment indicated by the cues in the experiment. For example, in empirical

555   studies of TWP in response to cues from predators, investigators often focus on inducible defenses, e.g.

556   behavioral or morphological traits which have been shown to increase survivorship when offspring are

557   in the presence of predators. In such cases, it is reasonable to assume that those traits would be more

558   strongly expressed if a subject's estimate of the value of an environmental state that contributes to

559   predation risk (e.g. predator density) was high than if it was low. In contrast, analyses of offspring

560   information-states are much less useful for predicting the plasticity of traits for which the expected

561   adaptive response to different information states is unknown or uncertain.

562   However, if a cue is information-only, if the adaptive phenotypic response to that cue is clear,

563   and if one has a reasonable idea about the relative reliability of the information provided by the

564   conditions in the different treatments, then these models can provide a useful benchmark against which

565   to compare the patterns for offspring trait values observed in empirical studies of TWP. For instance, if

566   parents and offspring are both exposed to the same cues from predators from birth to maturity, if one

567   measures inducible traits known to improve survivorship in the presence of that predator, and if it is

568   reasonable to assume that the cues in the P treatment and the cues in the N treatment are equally

569   reliable, then the models in the current paper predict a 'step-up' pattern for offspring trait values, in

570   which the values for an antipredator trait for the PN group are either the same or lower than the values

571   for the NP group (see Figs 1b and 4b). In addition, if information from the field indicates that the

572   environmental state of interest might change between the parental and offspring generations, one

573   would expect the trait values for the NP group to be higher than the trait values for the PN group.

574   An example of an experiment for which these conditions appear to be satisfied is a classic study

575   of TWP in which *Daphnia cucullata* parents and offspring were exposed to kairomones from a predator

576   (*Chaoborus flavicans*) from birth to first reproduction, and then relative helmet length was measured at

577   the age of first reproduction in the offspring [2]. Other experiments have shown that kairomones from

578   *C. flavicans* induce the development of larger helmets in *D. cucullate* [47], and that relatively large

579   helmets protect juvenile and adult *D. cucullata* from this predator [48]. In addition, field studies of *C.*

580   *flavicans* indicate that the risk it poses to *Daphnia* spp. varies within seasons across the temporal scales

581   that might encourage the devaluation of information from parents [49]. Finally, continuous exposure of

582   kairomones from a predator from birth to maturity in a P treatment is typically assumed to provide

583   reasonably reliable information about the density of that predator, while the absence of cues from the

584   predator from birth to maturity in an N treatment is assumed to provide comparably reliable

585   information indicating that the density of that predator is low. As predicted by the models described

586   herein under this set of conditions Agrawal et al. [2] reported a step-up pattern (NN < PN < NP < PP), in

587   which the trait values for all four groups were significantly different from one another.

588   Finally, the current study shows how an appreciation of the ways that information from

589   different sources is expected to combine within and across generations reveals a number of questions

590   that investigators might want to consider when they are planning or interpreting the results of empirical

591   studies of TWP in response to inductive cues. These are summarized as follows:

592   1) Are the inductive cues information-only, or could the inductive experiences also have direct, lasting

593   effects on the somatic states of either the parent or their offspring? Insights from models of

594   development based on information-updating are currently most useful for predicting trait values when

595   cues are information-only.

596   2) Are the conditions in the different treatments likely to provide equally reliable information about a

597   state of the environment, or are the conditions in one treatment likely to provide much more reliable

598   information than those in the other treatment? As was shown here and in [25], we expect the patterns

599   of offspring estimates in TWP studies to dramatically differ in these two situations.

600   3) Are parents and offspring exposed to the same cues for the same period of time? As is shown in the

601   current article, all else being equal, differences in the duration of cue-exposure for parents and offspring

602   are expected to affect the patterns of offspring estimates, especially if the cues in the different

603   treatments are equally reliable.

604   4) Is there strong existing support for the assumption that a particular response in a particular trait to a

605   particular cue is likely to be adaptive? In such cases, it is more likely that differences among the

606   treatment groups in offspring information states at the end of the experiment will be related to

607   differences among those groups in the trait values expressed by the offspring at the end of the

608   experiment.

609   In addition, our results indicate that it may not be necessary to invoke assumptions about

610   developmental constraints, costs of sampling, or the fitness consequences of trait values of offspring to

611   account for at least some of variation in results observed in empirical studies of TWP. Instead, we have

612   shown that even if we restrict ourselves to experiments with information-only cues, we should expect to

613   observe considerable variation in their results, as a function of variation in parental priors, the reliability

614   of the cues in the different treatments, differences in the duration of cue-exposure for parents and

615   offspring, and the extent to which information from parents was either devalued or degraded in

616   comparison to information from offspring.

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Acknowledgments

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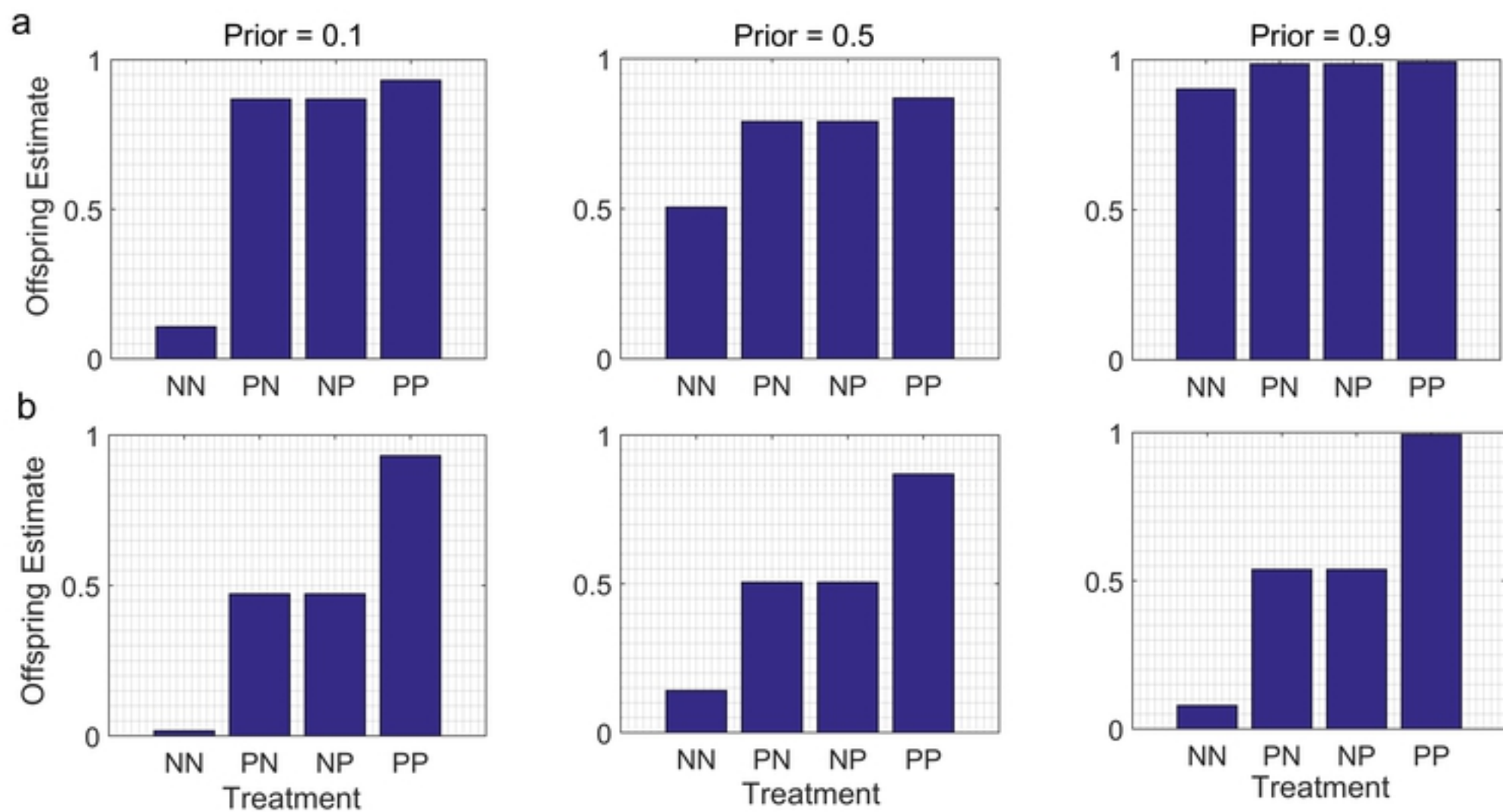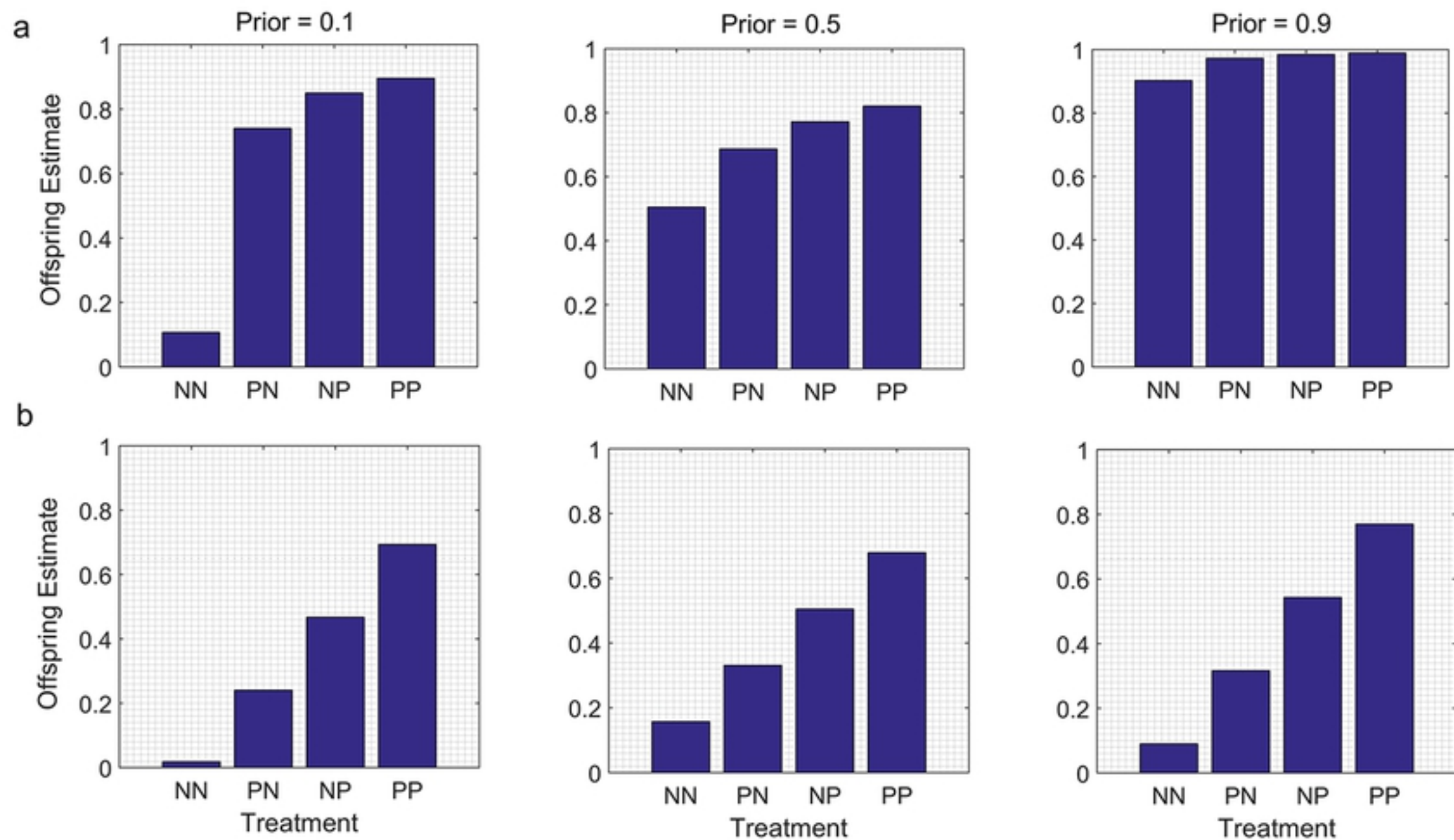740   spring. Journal of Limnology. 2018;77(2):309-15. doi: 10.4081/jlimnol.2018.1709.
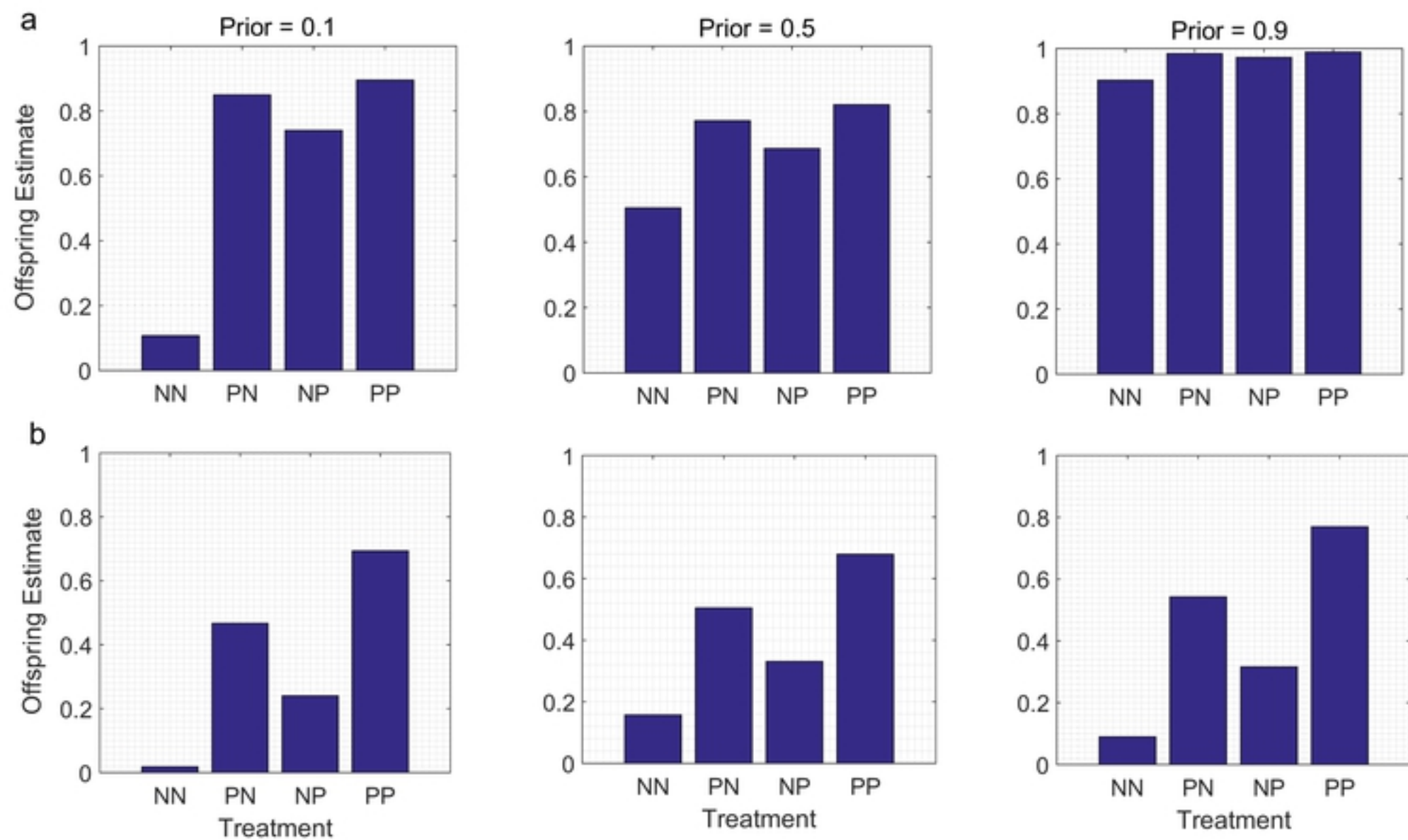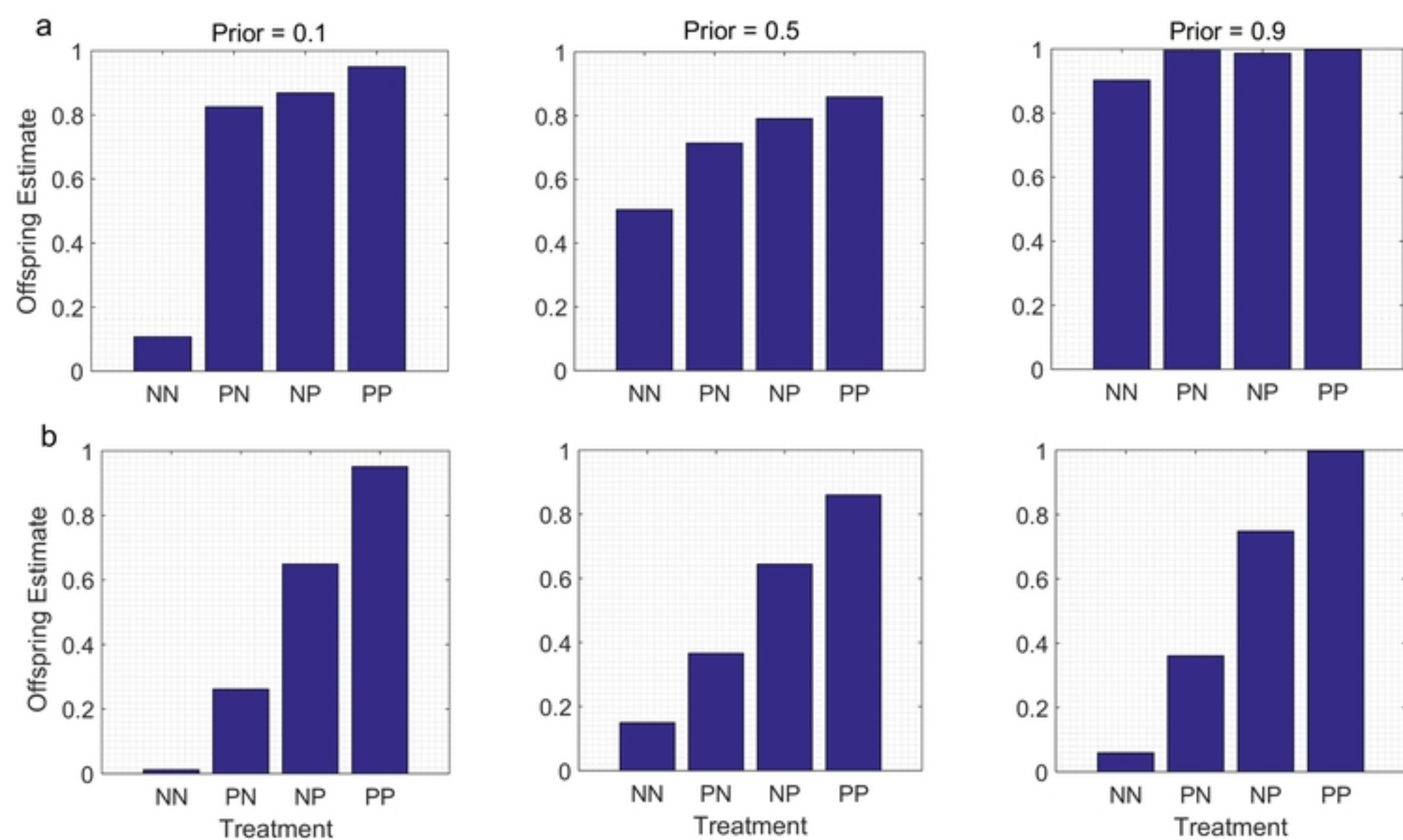
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Figure 1

Figure 2

Figure 3

Figure 4