



HAL
open science

The dynamics of sexually antagonistic coevolution and the complex influences of mating system and genetic correlation

Roger Härdling, Kristina Karlsson

► **To cite this version:**

Roger Härdling, Kristina Karlsson. The dynamics of sexually antagonistic coevolution and the complex influences of mating system and genetic correlation. *Journal of Theoretical Biology*, 2009, 260 (2), pp.276. 10.1016/j.jtbi.2009.05.024 . hal-00554617

HAL Id: hal-00554617

<https://hal.science/hal-00554617>

Submitted on 11 Jan 2011

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Author's Accepted Manuscript

The dynamics of sexually antagonistic coevolution and the complex influences of mating system and genetic correlation

Roger Härdling, Kristina Karlsson

PII: S0022-5193(09)00244-6
DOI: doi:10.1016/j.jtbi.2009.05.024
Reference: YJTBI5574



www.elsevier.com/locate/jtbi

To appear in: *Journal of Theoretical Biology*

Received date: 4 March 2009
Revised date: 20 May 2009
Accepted date: 21 May 2009

Cite this article as: Roger Härdling and Kristina Karlsson, The dynamics of sexually antagonistic coevolution and the complex influences of mating system and genetic correlation, *Journal of Theoretical Biology*, doi:[10.1016/j.jtbi.2009.05.024](https://doi.org/10.1016/j.jtbi.2009.05.024)

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting galley proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

1 **Title**

2 The dynamics of sexually antagonistic coevolution and the complex influences of
3 mating system and genetic correlation

4

5

6 **Authors and affiliations**

7 Roger Härdling^{a1} and Kristina Karlsson^{b*}

8 ^{ab}Section for Animal Ecology, Ecology Building, Lund University, SE-223 62 Lund,
9 Sweden.

10 ^aroger.hardling@zoekol.lu.se, Phone: +46-46-222 79 26 Fax: +46-46-222 47 16

11 ^bkristina.karlsson@zoekol.lu.se, Phone: +46-46-222 36 13 Fax: +46-46-222 47 16

12 ¹Present address: Cykelvägen 4, SE-24750, Dalby, Sweden.

13 rogerhardling@hotmail.com, +46 (0)706985101

14 *To whom correspondence should be addressed

15

16

17

18

19

20

21

22

23

24

25 **Abstract**

26

27 Sexual conflict has been proposed to be a mediator of speciation but recent theoretical
28 work, as well as empirical studies, suggests that sexual conflict may also be able to
29 prevent speciation and to preserve genetic polymorphism within a species. Here, we
30 develop a population genetic model and study the effects of sexual conflict in a
31 polymorphic population. The morphs mate assortatively based on different sexually
32 antagonistic traits and females are assumed to suffer a cost when the proportion of
33 matching males is high. We consider the model in two different mating systems;
34 promiscuity and polygyny. Our results show that genetic polymorphism may be
35 maintained through negative frequency dependent selection established by assortative
36 mating and female conflict costs. However, the outcome significantly differs between
37 mating systems. Furthermore, we show that indirect selection may have profound
38 effects on the evolutionary dynamics of a sexual conflict.

39

40

41

42

43

44

45

46

47 **Keywords:** assortative mating, genetic polymorphism, indirect selection, sexual

48 conflict, speciation

49 1. Introduction

50

51 Several studies have shown that sexual conflict may lead to genetic differentiation,
52 reproductive isolation and even speciation (Holland and Rice, 1999; Arnqvist et al.,
53 2000; Martin and Hosken, 2003; reviewed in Gavrilets and Hayashi, 2005). The direct
54 cause of these processes are thought to be sexually antagonistic traits that promote the
55 sexes' differing evolutionary interests, e.g. male antagonistic traits may tend to increase
56 male mating rate, while female conflict adaptations may tend to decrease mating rate.
57 Examples from the literature of such antagonistic traits include seminal proteins and the
58 ability to displace sperm in *Drosophila* (Rice W.R., 1996; Clark and Begun, 1998;
59 Clark et al., 1999) and grasping and anti-grasping morphologies in water striders
60 (Arnqvist and Rowe, 2002a; Arnqvist and Rowe, 2002b) and in diving beetles (Bergsten
61 and Miller, 2007).

62 The male and female antagonistic traits are usually termed persistence and
63 resistance traits, respectively, and a common assumption is that any given persistence
64 (or resistance) trait may be more or less efficient, dependent on the prevailing average
65 resistance (persistence) trait in the female (male) population (Gavrilets 2000). The
66 antagonistic traits may in other words "match" each other more or less well which
67 determines the "compatibility" of a male and a female (Gavrilets, 2004). Under sexual
68 conflict theory, females are expected to experience lower fitness when they are more
69 exposed to mating related costs, which is when the proportion of males with matching
70 antagonistic traits is highest. It will thus be in the interest of females to evolve away
71 from this point, while it is in the males interest to increase compatibility with the female
72 traits (Holland and Rice, 1998; Gavrilets, 2000). As a result, resistance and persistence

73 traits may co-evolve in a perpetual sexual arm race (but see Parker, 1979). When
74 captured in such arms race, allopatric populations could diverge, or evolve in the same
75 directions but under different rates, eventually becoming reproductively isolated
76 (Gavrilets, 2000; Gavrilets and Waxman, 2002).

77 Speciation seems, however, not to be the only possible consequence of genetic
78 diversification due to sexual conflict (Gavrilets and Waxman, 2002; Haygood, 2004;
79 Härdling and Bergsten, 2006). With a genetic model, Gavrilets and Waxman (2002)
80 initially found that sexual conflict sometimes may result in female polymorphism.
81 Maintenance of polymorphism was further investigated by Härdling & Bergsten (2006)
82 using a phenotypic model where both sexes were polymorphic and where mating was
83 positively assortative between morphs with matching resistance and persistence traits.
84 In this system, polymorphism could be maintained by sexual conflict when the
85 corresponding male and female traits were genetically correlated. Besides theoretical
86 models, polymorphism is suggested to be maintained by sexual conflict also in natural
87 populations e.g. in diving beetles (Härdling and Bergsten, 2006) and damselflies
88 (Svensson et al., 2005).

89 Assortative mating inevitably leads to joint inheritance of the traits that constitute
90 the basis for mate matching, and establishes a genetic correlation between these traits
91 (Lande, 1981; Gavrilets, 2004). A consequence of such correlation is that if one sex
92 experiences strong selection, the opposite sex may be affected through indirect selection
93 (Lande, 1981). While indirect selection is instrumental in models of sexual selection
94 (Andersson, 1994), sexual conflict theory is primarily based on direct selection effects,
95 and indirect selection is often thought to be less important (Kirkpatrick and Barton,
96 1997; Kokko, 2005). However, since assortative mating must exist between males and

97 females with matching resistance and persistence traits, the role of indirect selection in
98 sexual conflict systems is important to consider.

99 Further, factors influencing indirect selection may interact in complex ways;
100 genetic correlation is dependent on assortative mating, which is a feature of the mating
101 system (Falconer and MacKay, 1989), but the idiosyncrasies of the mating system may
102 also affect direct selection. The opportunity for selection may differ between the sexes
103 in different mating system depending on the fitness variance among members of each
104 sex (Shuster and Wade, 2003). For example, polygyny and monogamy cause differing
105 direct selection on males because males have different expected mating probability
106 dependent on mating system (Gavrilets, 2004). The properties of the mating system may
107 thus be an important aspect to consider when addressing the significance of indirect
108 selection in sexual conflict regimes.

109 Here we investigate the evolutionary dynamics of sexual conflict and antagonistic
110 conflict adaptations while taking into account genetic inheritance of conflict adaptations
111 and differences in mating systems. We focus on the links between mating behaviour,
112 assortative mating and linkage disequilibrium and model both promiscuous and
113 polygynous mating systems. Our model shares some assumptions with the model by
114 Härdling & Bergsten (2006) but their model addressed different questions and did not
115 specify the cause of indirect selection unlike the present model. We show that mating
116 system characteristics are typically decisive for the antagonistic coevolutionary process
117 in general and the outcome with respect to coexistence of multiple male and female
118 conflict adaptations in particular.

119

120 **2. The model**

121

122 We consider a population where both males and females are polymorphic. Males
 123 occur in two distinct morphs a' and b' , and females are type a or b . We assume that
 124 morph is determined by two different loci with sex-specific expression, and that the
 125 evolutionary dynamics can be described by haploid inheritance. In males, allele z_1 codes
 126 for morph a' and allele z_2 for morph b' . In females, allele y_1 codes for morph a and y_2
 127 for morph b . Genetic recombination occurs at rate r . We will analyse the model under
 128 two different assumptions about the mating system; that both sexes may mate
 129 repeatedly during one season (promiscuity), or that only males mate repeatedly
 130 (polygyny).

131

132 *2.1. Promiscuity*

133

134 Assume that both males and females mate repeatedly during one season (Fig. 1a).
 135 The population has a type-matching mating system similar to the one described by Nei
 136 (1976) and Kirkpatrick (1982). Specifically, the mating probability in encounters
 137 between a' males and b females, and between b' males and a females is only a fraction
 138 k of that in (a, a') and (b, b') combinations. This difference may be due to morph-
 139 specific female resistance, or differential male persistence to female morphs, but the
 140 model does not depend on any such specific assumption.

141

142

143

144

Let x_1 to x_4 denote the population frequencies of the different genotypes z_1y_1 ,
 z_1y_2 , z_2y_1 , z_2y_2 . With these assumptions, the frequency of different mating combinations
 are given by equations (1) to (4), where $Q(a', a)$ denotes the frequency of (a', a)
 matings and so on.

145

$$146 \quad Q(a', a) = (x_1 + x_2)(x_1 + x_3) / \psi \quad (1)$$

$$147 \quad Q(a', b) = k(x_1 + x_2)(x_2 + x_4) / \psi \quad (2)$$

$$148 \quad Q(b', a) = k(x_3 + x_4)(x_1 + x_3) / \psi \quad (3)$$

$$149 \quad Q(b', b) = (x_3 + x_4)(x_2 + x_4) / \psi \quad (4)$$

150

151 Where $\psi = (x_1 + x_2)(x_1 + x_3) + k(x_1 + x_2)(x_2 + x_4) + k(x_3 + x_4)(x_1 + x_3) + (x_3 + x_4)(x_2 + x_4)$.

152 Thus the deviation from random mating under this mating system can be expressed by
 153 multiplying the random mating rate expression with one of four factors; A , kA , B and kB
 154 (see Table 1), where $A = B = 1 / \psi$ (Table1). By expanding equations (1)-(4) we derive
 155 mating rates U_{ij} in Table 1 for x_i, x_j – matings (Table 1).

156 Matching-based assortative mating always gives a direct fitness advantage to
 157 males that are “adapted to” or most compatible with the most frequent female morph
 158 (Gavrilets 2004). This means that regardless of which female morph that is most
 159 common, the corresponding male morph has the higher mating frequency. Let $p = (x_1 +$
 160 $x_2)$ and $q = (x_1 + x_3)$. Then, in promiscuous mating systems, males of the a' morph has
 161 higher mating rate than b' males when

162

$$163 \quad \frac{Q(a', a) + Q(a', b)}{p} > \frac{Q(b', a) + Q(b', b)}{1 - p} \quad (5)$$

164

165 This is true when

166

$$167 \quad q > \frac{1}{2} \quad (6)$$

168

169 i.e. when a females are the most common.

170

171 2.2. Polygyny

172

173 Assume that females only mate once, but that males may mate repeatedly during
 174 one season (Fig. 1b). Mating probability is assumed to be based on phenotype matching,
 175 as before. Then the mating probabilities (P , to distinguish this case from promiscuity)
 176 are the following:

177

$$178 \quad P(a', a) = (x_1 + x_2)(x_1 + x_3) / (x_1 + x_2 + k(x_3 + x_4)) \quad (7)$$

$$179 \quad P(a', b) = k(x_1 + x_2)(x_2 + x_4) / (k(x_1 + x_2) + x_3 + x_4) \quad (8)$$

$$180 \quad P(b', a) = k(x_3 + x_4)(x_1 + x_3) / (x_1 + x_2 + k(x_3 + x_4)) \quad (9)$$

$$181 \quad P(b', b) = (x_3 + x_4)(x_2 + x_4) / (k(x_1 + x_2) + x_3 + x_4) \quad (10)$$

182

183 Thus the A and B factors for multiplication are for the promiscuous mating system
 184 changed to

185

$$186 \quad A = (p + k(1 - p))^{-1}, \quad (11)$$

$$187 \quad B = (kp + (1 - p))^{-1}. \quad (12)$$

188

189 Mating rates U_{ij} are calculated in a similar way as for promiscuity. The selective effect
 190 of polygyny differs from promiscuity. In a polygynous mating system, the a' morph has
 191 higher mating rate than b' males when

192

$$193 \quad q > \frac{p + k(1 - p)}{1 + k} \quad (13)$$

194

195 If $k < 1$, i.e. mating is non-random, the RHS of (13) is lower than $\frac{1}{2}$ whenever $p < \frac{1}{2}$ (cf.

196 Eq. (6)).

197

198 *2.3. Sexual conflict costs*

199

200 Female fitness (either fecundity or viability) is negatively affected by male
 201 interference, such as harassment (Schlupp et al., 2001; Muhlhauser and Blanckenhorn,
 202 2002; Sakurai and Kasuya, 2008), seminal fluid toxicity (Chapman et al., 1995) or mate
 203 guarding (Jormalainen et al., 2001). The costs imposed on females are assumed to be
 204 larger if the proportion of males in the population with matching mating adaptations is
 205 high. Thus, using linear cost functions, the fitness for female morph a and b is $W_a = 1 -$
 206 $s(x_1 + x_2)$ and $W_b = 1 - s(x_3 + x_4)$, respectively. The factor s determines female sensitivity
 207 to male harassment ($0 \leq s \leq 1$).

208

209 *2.4. Evolutionary dynamics*

210

211 Using the standard mating table approach (Table 1), recursion equations
 212 describing the dynamics of the four-genotype system can be derived (eg. Rice, 2004).
 213 The per generation change in allele frequency is for the four genotypes as follows:

214

$$215 \quad \Delta x_1 = \frac{x_1(\omega_1 - \bar{\omega}) - r(kx_1x_4 - x_2x_3)(\frac{1}{2}BW_b + \frac{1}{2}AW_a)}{\bar{\omega}} \quad (14)$$

$$216 \quad \Delta x_2 = \frac{x_2(\omega_2 - \bar{\omega}) + r(kx_1x_4 - x_2x_3)(\frac{1}{2}BW_b + \frac{1}{2}AW_a)}{\bar{\omega}} \quad (15)$$

$$217 \quad \Delta x_3 = \frac{x_3(\omega_3 - \bar{\omega}) + r(kx_1x_4 - x_2x_3)(\frac{1}{2}BW_b + \frac{1}{2}AW_a)}{\bar{\omega}} \quad (16)$$

$$218 \quad \Delta x_4 = \frac{x_4(\omega_4 - \bar{\omega}) - r(kx_1x_4 - x_2x_3)(\frac{1}{2}BW_b + \frac{1}{2}AW_a)}{\bar{\omega}} \quad (17)$$

219 where

220

$$221 \quad \omega_1 = W_a A x_1 + \frac{1}{2}(W_a A + kW_b B)x_2 + \frac{1}{2}W_a A(1+k)x_3 + \frac{1}{2}k(W_a A + W_b B)x_4 \quad (18)$$

$$222 \quad \omega_2 = \frac{1}{2}(W_a A + kW_b B)x_1 + kW_b B x_2 + \frac{1}{2}(W_a A + W_b B)x_3 + \frac{1}{2}W_b B(1+k)x_4 \quad (19)$$

$$223 \quad \omega_3 = \frac{1}{2}W_a A(1+k)x_1 + \frac{1}{2}(W_a A + W_b B)x_2 + kW_a A x_3 + \frac{1}{2}(kW_a A + W_b B)x_4 \quad (20)$$

$$224 \quad \omega_4 = \frac{1}{2}k(W_a A + W_b B)x_1 + \frac{1}{2}W_b B(1+k)x_2 + \frac{1}{2}(kW_a A + W_b B)x_3 + W_b B x_4 \quad (21)$$

225

226 and

227

$$228 \quad \bar{\omega} = x_1\omega_1 + x_2\omega_2 + x_3\omega_3 + x_4\omega_4 \quad (22)$$

229

230 Note that with random mating ($k = 1$), then $A = B = 1$ and the system is reduced to a

231 standard two locus dynamic system with frequency dependent female fitness (e.g. Rice,

232 2004).

233

234 3. Results

235

236 At evolutionary equilibrium, each sex is composed of two morphs in equal
 237 frequencies ($a = b = 1/2$, and $a' = b' = 1/2$). This result holds for both the polygynous and
 238 the promiscuous mating system. The linkage disequilibrium D at equilibrium is

$$240 \quad D = \frac{2\sqrt{k} - k - 1}{4(k - 1)}. \quad (23)$$

241 Thus, neither recombination rate (r) nor female conflict costs (s) influences the
 242 equilibrium location or the genetic covariance at equilibrium. Fig. 2 shows
 243 disequilibrium D as a function of k , the mating probability in (a, b') and (b, a')
 244 encounters.

245 The stability properties of the internal equilibrium (where $p = 1/2$, $q = 1/2$) can
 246 be studied by performing a local analysis of the four-genotype dynamic system. All
 247 eigenvalues of the Jacobian of the dynamic system (Eqs. 14 – 17) when analysed at the
 248 point of equilibrium should have an absolute value lower than unity for equilibrium to
 249 be convergence stable (Edelstein-Keshet, 1988). A graphic presentation of the local
 250 analysis, for both mating systems with $r = 1/2$, is presented in Fig. 3, showing isoclines of
 251 the maximum eigenvalue for the four-allele system, in the parameter area
 252 $0 < s < 1$, $0 < k < 1$.

253 In a promiscuous mating system, equilibrium with maintenance of all morphs is
 254 stable when $s > 1 - k$ (Figs. 3a, 4a). This condition demonstrates the opposing forces of
 255 assortative mating and sexual conflict costs. Increasing the female conflict cost
 256 parameter (s) make the costs larger and more strongly frequency dependent. Thus at any
 257 one time the least common female morph is usually favoured by natural selection
 258 (because fewer males are adapted to them, or equivalently because these females have

259 defence against the most common male genotypes). This stabilises the internal
260 equilibrium.

261 More pronounced assortative mating (low k) increases direct selection on males
262 and the genetic correlation between the sexes, so that indirect selection on females
263 increases (Lande, 1981).. Stronger linkage disequilibrium couples the dynamics of the z
264 and y alleles and makes the female morph frequency evolution follow the evolution of
265 the male compatible morphs. In other words, if a females are common, assortative
266 mating causes direct selection favouring a' males and via disequilibrium indirect
267 selection favouring a females. Thus the most common male and female genotypes are
268 favoured in a feedback fashion so that the equilibrium is destabilized (Fig. 4b).

269 If the internal equilibrium is unstable ($s < 1 - k$, Fig. 3a) the population
270 eventually becomes fixed for either genotype z_1y_1 or z_2y_2 (Fig. 4b). Males and females
271 then have morphs (a', a) or (b', b) . These are “compatible” i.e. maximises mating
272 probability, which is in line with male interests but negative for females.

273 If the species has a polygynous mating system, the internal equilibrium is always
274 convergence stable independent on female conflict costs and strength of assortative
275 mating (Fig. 3b). Moreover, increasing mating assortativeness strengthens stability, in
276 contrast to then promiscuous case (Fig. 3b). This counterintuitive result arises because
277 of the direct selection pressure the mating system imposes on male morphs (13).
278 Condition (13) implies that when either of the male morphs is rare, it is favoured by
279 selection under a wider range of conditions (female morph frequencies) than in the case
280 of promiscuity. Thus the polygynous mating system introduces an element of stabilizing
281 frequency dependence that leads to stronger evolutionary stability in the polygynous
282 case (Fig. 3b).

283

284 **4. Discussion**

285

286 In this paper, we model the effect of sexual conflict on the evolutionary dynamics
287 of a genetically polymorphic population. Two alternative outcomes exist; either both
288 sexes maintain a stable genetic polymorphism or polymorphism is lost in both sexes, as
289 some alleles become fixed in the population. The detailed results are complex and
290 contingent on factors such as mating system and degree of assortative mating

291 In our model, polymorphism is maintained through negative frequency dependent
292 selection in combination with indirect selection, caused both by assortative mating and
293 female sexual conflict costs. Assortative mating is based on trait compatibility between
294 two pairs of male and female morphs. Examples of such traits are the grasping and anti-
295 grasping morphologies developed in gerrids (Arnqvist and Rowe 2002b; Arnqvist and
296 Rowe 2002a) and diving beetles (Bergsten and Miller 2007). Since mating is assumed
297 to entail a cost for females, e.g. in energy expenditure (Watson et al., 1998), immune
298 suppression (Fedorka and Zuk, 2005), reduced lifespan (Fowler and Partridge, 1989) or
299 reduced lifetime fitness (Sakurai and Kasuya, 2008), females with the lowest mating
300 frequency have a selective advantage. Males, on the other hand, will have highest
301 mating advantage if their phenotype matches that of the most common female morph.
302 The female morph which is compatible with the most prevailing male morph will be
303 more exposed to mating attempts and will consequently suffer more mating costs.
304 Eventually this morph will decrease in frequency due to the direct negative effect that
305 mating has for females. Thus direct mating costs generate negative frequency dependent
306 selection between the female morphs.

307 Since assortative mating between morphs establishes a genetic correlation, the
308 corresponding male morph will be affected by the female mating costs through indirect
309 selection (Lande, 1981). As the female morph decreases in frequency, the compatible,
310 most common, male morph will also decrease. The male morph decreases in frequency
311 until it becomes the least common morph, at which point the negative direct selection
312 on the female morph will be reduced and this female morph now has the selective
313 advantage. The female morph will thus begin to increase in frequency until it becomes
314 the most common morph and its matching male morph gets the selective advantage,
315 increases to majority and again imposes a too high cost for the female morph. Indirect
316 selection is therefore the cause of fluctuations in frequency between the male morphs,
317 which is necessary for the continued fluctuation of female morphs. As a result, male and
318 female conflict adaptations reach the stable point after convergent cycles around the
319 equilibrium (Fig. 4a) (Gavrilets, 2000; Gavrilets and Waxman, 2002; Härdling and
320 Bergsten, 2006).

321 Mating system characteristics may, however, alter the basic scenario described
322 above. With completely random mating, the female morph that suffers most from male
323 harassment will become lost due to costs from sexual conflict. Because no genetic
324 correlation is created, and because random mating is non-selective for male morphs (i.e.
325 it is not a source of selection on males) male morph frequencies do not change
326 evolutionarily in the case when mating is random. Thus, non-random mating and the
327 resulting genetic correlation between compatible pairs is a prerequisite for the
328 coevolutionary dynamics and the stable internal equilibrium (Härdling and Bergsten,
329 2006). It should be pointed out that the genetic correlation does not have to be
330 particularly strong to have this important effect. In the modelled polygynous mating

331 system, arbitrarily low genetic correlations ensure stability of the equilibrium point (Fig
332 3b). And in the promiscuous case, low genetic correlations cause stability under most
333 female cost conditions (low k in Fig. 3a).

334 Stable equilibrium, with genetic polymorphism in both males and females, may be
335 reached both with a promiscuous and a polygynous mating system. In both cases,
336 increasing female mating cost tends to increase stability of the polymorphism, all else
337 equal (Figs. 3a and b). Costly mating can therefore help preserve genetic variation. For
338 the polygynous population (Fig. 3b), but not for the promiscuous, stability is further
339 strengthened with increased degree of assortative mating. This difference between the
340 mating systems is explained by how selection operates on males. In a promiscuous
341 population (Eq. 6), males of e.g. morph a' (frequency p) are only favoured by direct
342 selection if a females (frequency q) are in majority; ($q > 1/2$). In the polygynous case
343 (Eq. 13) the condition is close to ($q > 1/2$) when assortative mating is very low ($k \approx 1$)
344 but if the degree of assortative mating is increased, the parameter interval with selective
345 advantage for males is widened. In the extreme case of perfect nonrandom mating ($k =$
346 0), males of morph a' (frequency p) are favoured by direct selection if a females
347 (frequency q) are more frequent among females than a' males among males (i.e. if $q >$
348 p). Thus, rare male morphs have a mating rate advantage over a wider parameter range
349 in the polygynous system than in the promiscuous system. The strong selection on
350 males reinforces the negative frequency dependent selection caused by female conflict
351 costs, which stabilises the polymorphic equilibrium

352 Unstable equilibrium (Fig. 4b), where one morph pair sometimes goes to fixation,
353 is only found for the promiscuous population since in this mating system the stabilising
354 effect from female conflict costs may be offset by assortative mating. When non-

355 random mating exceeds mating costs, males "matching" the most common female
356 morph will always be favoured by selection (Eq.6). This is because strong direct
357 selection on the male morph affects females through linkage disequilibrium (Eq. 24). As
358 a result, the direct selection effect on female morph frequencies through mating costs is
359 outweighed and female morphs suffering from direct sexual conflict costs will still
360 increase in frequency. The most common morph pair will therefore increase in
361 frequency via indirect selection and eventually become genetically fixed. In a
362 promiscuous mating system, the evolutionary outcome therefore depends on whether
363 direct selection is stronger on males (because of assortative mating) or on females
364 (because of conflict costs) and in both cases the opposite sex is "dragged along" by
365 indirect selection. The unstable case is comparable to the dynamics of chase-away
366 selection and antagonistic arms races (Holland and Rice 1998), viz. frequent changes in
367 male and female allele frequencies. However, in our model, stable morph frequencies
368 result under a wider parameter space and may be wide spread also in natural populations
369 (Svensson et al., 2005; Härdling and Bergsten, 2006; Gosden and Svensson, 2007).

370 The condition for unstable equilibrium, $s < 1 - k$, can be interpreted as a
371 condition for sympatric speciation comparable to the result by Udovic (1980). The
372 Udovic model predicts sympatric speciation when the cumulative strength of viability
373 selection (v) on heterozygotes and assortative mating (a) is larger than a threshold value
374 ($v + a > 1$). In our model, the strength of assortative mating is $(1 - k)$, and s is the fitness
375 loss of females that mate with harmful males. Thus, decreasing female fitness costs
376 causes population differentiation in our model, while in contrast the Udovic model
377 predicts speciation with increased viability costs (Udovic, 1980; Gavrillets, 2004).

378 As we have seen, whether a population will stay polymorphic or will lose genetic
379 variation depends on the balance between female conflict costs and assortative mating,
380 together with the particulars of its mating system. For all outcomes however, indirect
381 selection has a crucial role. This gives two insights; first that indirect selection may be
382 of importance in sexual conflict systems, with potential to influence the dynamics just
383 like with direct fitness effects. The significance of indirect selection does not question
384 the presence of a sexual conflict; instead it contributes with an additional dimension to
385 the dynamics initiated by direct mating costs. Second, the result illustrates the
386 intersexual dynamics, showing how the impacts on one sex inevitably affect the other.
387 Indeed it is not possible to assign winners and losers of sexual conflict since the sexes
388 are mutually dependent on each other for their reproductive success (Arnqvist and
389 Rowe, 2005). In our model, assortative mating is ultimately based upon matching
390 between dimorphic alleles at two sexspecific loci, although we expect similar results
391 also for a population with more than two different alleles (i.e. with more than two
392 compatible morph pairs) since it is the establishment of genetic correlation and the
393 potential for indirect selection that is fundamental.

394 We have here considered two mating system extremes (Figs. 2a and b),
395 promiscuous in one end and polygynous in the other, but for natural populations the
396 reality may be somewhere in between. Theory predicts that the expressed mating system
397 depends on the availability of defendable resources (Emlen and Oring, 1977). The
398 features of the prevailing mating system could therefore probably vary between years or
399 over seasons, depending on ecological factors such as food access or availability of
400 suitable habitat, making the long-term evolutionary consequences of the conflict
401 difficult to predict. Rapid environmental change could thus potentially affect the

402 outcome of sexual conflict through mating system, making the outcome of sexual
403 conflict even more complex and unpredictable for populations affected by habitat
404 destruction and population decreases.

405 Sexual conflict has been suggested to be a strong “engine of speciation” (Rice,
406 1998; Arnqvist et al., 2000) since coevolution between the sexes may be very rapid and
407 often involves reproductive traits, enhancing the chance for reproductive isolation to
408 evolve (Rice, 1998). Our model shows, however, that sexual conflict also may act to
409 maintain the genetic variation below the species level, so that multiple resistance-
410 persistence trait combinations may frequently be able to coexist without leading to
411 coevolutionary chases or races. This is interesting to consider as an alternative outcome
412 of sexual conflict to sexual conflict driven speciation, which may be a process that only
413 occurs under restricted conditions.

414 In conclusion, the current model shows how selection acts on populations with
415 multiple resistance-persistence trait combinations. We show that the interaction between
416 conflict cost and the inevitable assortative mating in conflicts affect the evolutionary
417 outcome. Of major importance for the outcome is the mating system characteristics and
418 its significance should always be considered for better understanding of sexual
419 conflicts, both in theoretical models and when studying natural populations. Phenotypic
420 and genetic polymorphism are maintained at most of the here investigated parameter
421 space, indicating that sexual conflict, under these assumptions, frequently restrain
422 differentiation and preserve genetic variation within populations. With Rice’s (1998)
423 illustrative example of sexual conflict as a dancing couple forever attached to each other
424 in mind, the most representative result from our model is perhaps the mutually

425 dependence between the sexes and the consequences sexual costs and benefits have not
426 only for the exposed sex but for the entire population.

427

428 **Acknowledgments**

429 We would like to thank two anonymous referees and the Erik Svensson lab group
430 for useful comments on an earlier draft. R.H. wishes to thank the Swedish Research
431 council for funding during the time the study was made.

432

433 **References**

434

435 Andersson, M., 1994. *Sexual selection*, 1 ed. Princeton University Press, Princeton.

436 Arnqvist, G., Rowe, L., 2005. *Sexual Conflict*. Princeton University Press, Princeton, NJ.

437 Arnqvist, G., Edvardsson, M., Friberg, U., Nilsson, T., 2000. Sexual conflict promotes
438 speciation in insects. *Proceedings of the National Academy of Sciences of the*
439 *United States of America* 97(19), 10460-10464.

440 Arnqvist, G., Rowe, L., 2002a. Antagonistic coevolution between the sexes in a group of
441 insects. *Nature (London)* 415(6873), 787-789.

442 Arnqvist, G., Rowe, L., 2002b. Correlated evolution of male and female morphologies in
443 water striders. *Evolution* 56(5), 936-947.

444 Bergsten, J., Miller, K.B., 2007. Phylogeny of Diving Beetles Reveals a Coevolutionary
445 Arms Race between the Sexes. *PLoS ONE* 2(6), e522.

- 446 Chapman,T., Liddle,L.F., Kalb,J.M., Wolfner,M.F., Partridge,L., 1995. Cost of mating
447 in *Drosophila melanogaster* females is mediated by male accessory gland
448 products. *Nature (London)* 373(6511), 241-244.
- 449 Clark,A.G., Begun,D.J., 1998. Female genotypes affect sperm displacement in
450 *Drosophila*. *Genetics* 149(3), 1487-1493.
- 451 Clark,A.G., Begun,D.J., Prout,T., 1999. Female X male interactions in *Drosophila*
452 sperm competition. *Science (Washington D C)* 283(5399), 217-220.
- 453 Edelman-Keshet,L., 1988. *Mathematical models in biology*. McGraw-Hill, New York.
- 454 Emlen,S.T., Oring,L.W., 1977. *Ecology Sexual Selection and the Evolution of Mating*
455 *Systems*. *Science (Washington D C)* 197(4300), 215-223.
- 456 Falconer,D.S., MacKay,T.F.C., 1989. *Introduction to quantitative*
457 *genetics*. Pearson, Petaling Jaya, Malaysia.
- 458 Fedorka,K.M., Zuk,M., 2005. Sexual conflict and female immune suppression in the
459 cricket, *Allonemobius socius*. *Journal of Evolutionary Biology* 18(6), 1515-
460 1522.
- 461 Fowler,K., Partridge,L., 1989. A Cost of Mating in Female Fruit Flies. *Nature (London)*
462 338(6218), 760-761.
- 463 Gavrillets,S., 2004. *Fitness landscapes and the origin of species*. Princeton University
464 Press, Princeton, New Jersey.

- 465 Gavrilets,S., 2000. Rapid evolution of reproductive barriers driven by sexual conflict.
466 Nature (London) 403(6772), 886-889.
- 467 Gavrilets,S., Hayashi,T.I., 2005. Speciation and sexual conflict. *Evolutionary Ecology*
468 19(2), 167-198.
- 469 Gavrilets,S., Waxman,D., 2002. Sympatric speciation by sexual conflict. *Proceedings of*
470 *the National Academy of Sciences of the United States of America* 99(16),
471 10533-10538.
- 472 Gosden,T.P., Svensson,E.I., 2007. Female Sexual Polymorphism and Fecundity
473 Consequences of Male Mating Harassment in the Wild. *PLoS ONE* 2(6), e580.
- 474 Härdling,R., Bergsten,J., 2006. Nonrandom Mating preserves Intrasexual
475 Polymorphism and Stops Population Differentiation in Sexual Conflict. *The*
476 *American Naturalist* 167(3), 401-409.
- 477 Haygood,R., 2004. Sexual conflict and protein polymorphism. *Evolution* 58(7), 1414-
478 1423.
- 479 Holland,B., Rice,W.R., 1998. Perspective: Chase-Away Sexual Selection: Antagonistic
480 Seduction Versus Resistance. *Evolution* 52(1), 1-7.
- 481 Holland,B., Rice,W.R., 1999. Experimental removal of sexual selection reverses
482 intersexual antagonistic coevolution and removes a reproductive load.
483 *Proceedings of the National Academy of Sciences of the United States of*
484 *America* 96(9), 5083-5088.

- 485 Jormalainen,V., Merilaita,S., Riihimaki,J., 2001. Costs of intersexual conflict in the
486 isopod *Idotea baltica*. *Journal of Evolutionary Biology* 14(5), 763-772.
- 487 Kirkpatrick,M., 1982. Sexual selection and the evolution of female
488 mate choice. *Evolution* 36, 1-12.
- 489 Kirkpatrick,M., Barton,N., 1997. The strength of indirect selection on female mating
490 preferences. *Proceedings of the National Academy of Sciences of the United*
491 *States of America* 94(4), 1282-1286.
- 492 Kokko,H., 2005. Treat 'em mean, keep 'em (sometimes) keen: evolution of female
493 preferences for dominant and coercive males. *Evolutionary Ecology* 19, 123-
494 135.
- 495 Lande,R., 1981. Models of Speciation by Sexual Selection on Poly Genic Traits.
496 *Proceedings of the National Academy of Sciences of the United States of*
497 *America* 78(6), 3721-3725.
- 498 Martin,O.Y., Hosken,D.J., 2003. The evolution of reproductive isolation through sexual
499 conflict. *Nature (London)* 423(6943), 979-982.
- 500 Muhlhauser,C., Blanckenhorn,W.U., 2002. The costs of avoiding matings in the dung
501 fly *Sepsis cynipsea*. *Behavioral Ecology* 13(3), 359-365.
- 502 Nei,M., 1976. Mathematical models of speciation and genetic distance. In: Karlin,S.,
503 Nevo,E. (Eds.), *Population*
504 *genetics and ecology*. Academic Press, New York, pp. 723-768.

- 505 Parker,G.A., 1979. Sexual selection and sexual conflict. In: Blum,M.S., Blum,N.A.
506 (Eds.), Sexual selection and reproductive competition in insects. Academic
507 Press, London, pp. 123-166.
- 508 Rice W.R., 1996. Sexually antagonistic male adaptation triggered by experimental arrest
509 of female evolution. *Nature* 381, 232-234.
- 510 Rice,S.H., 2004. Evolutionary theory: mathematical and conceptual
511 foundations. Sinauer, Sunderland, MA.
- 512 Rice,W.R., 1998. Intergenomic Conflict, Interlocus Antagonistic Coevolution, and the
513 Evolution of Reproductive Isolation. In: Howard,D.J., Berlocher,S.H. (Eds.),
514 Endless forms: species and speciation. Oxford University Press, Oxford, pp. 261-
515 270.
- 516 Sakurai,G., Kasuya,E., 2008. The costs of harassment in the adzuki bean beetle. *Animal*
517 *Behaviour* 75(Part 4), 1367-1373.
- 518 Schlupp,I., Mc Knab,R., Ryan,M.J., 2001. Sexual harassment as a cost for molly
519 females: Bigger males cost less. *Behaviour* 138(2), 277-286.
- 520 Shuster,S.M., Wade,M.J., 2003. Mating systems and strategies. Princeton University
521 Press, Princeton.
- 522 Svensson,E.I., Abbott,J., Härdling R., 2005. Female Polymorphism, Frequency
523 Dependence, and Rapid Evolutionary Dynamics in Natural Populations. *The*
524 *American Naturalist* 165(5), 567-576.

525 Udovic,D., 1980. Frequency Dependent Selection Disruptive Selection and the
526 Evolution of Reproductive Isolation. American Naturalist 116(5), 621-641.

527 Watson,P.J., Arnqvist,G., Stallmann,R.R., 1998. Sexual conflict and the energetic costs
528 of mating and mate choice in water striders. American Naturalist 151(1), 46-58.

529

530 **Legends to figures**

531

532 **Figure 1.** Schematic view of the (a) promiscuous and (b) polygynous mating system
533 that appears in the model.

534

535 **Figure 2.** The linkage disequilibrium (D) between the x and y locus at the evolutionary
536 equilibrium (Eq. 23). Linkage disequilibrium is purely a function of the assortative
537 mating parameter k (Eq. 24) and is identical for both modelled mating systems.

538

539 **Figure 3.** Graphic representation of a local stability analysis of the equilibrium with
540 coexistence of all four genotypes (Eq. 23). The isoclines depict the absolute value of the
541 maximum eigenvalue of the recursion system (Eqs. 18 – 21). For stability, this value
542 should be lower than 1. The vertical axis measures female conflict costs (s). The
543 horizontal axes show degree of assortative mating, which is measured as $(1 - k)$ (see
544 text). Panel (a) shows the promiscuous mating system and here stability requires that $s >$
545 $(1 - k)$. Panel (b) shows the polygynous mating system and here the internal equilibrium
546 is always stable. The figure is drawn for a recombination rate $r = \frac{1}{2}$.

547

548 **Figure 4.** Two examples of the dynamics of the promiscuous mating system, showing
549 the coevolution of male and female conflict adaptations. Panel (a) shows a case where
550 the internal equilibrium is stable. When the population is initiated at a point with near
551 fixation of a particular pair of matching male and female conflict adaptations,
552 antagonistic coevolution leads, through direct selection effects, the phenotype
553 frequencies in a cyclic fashion towards the equilibrium. In (b) the equilibrium is
554 unstable because of strong assortative mating. Disequilibrium leads to indirect selection
555 on females that overrides direct selection and leads to either of the two points with
556 matching male and female conflict adaptations. Parameter values: (a) $s = 0.5$, $k = 0.4$, r
557 $= 0.5$; (b) $s = 0.4$, $k = 0.5$, $r = 0.5$.

558

559

560

561

562

563

564

565

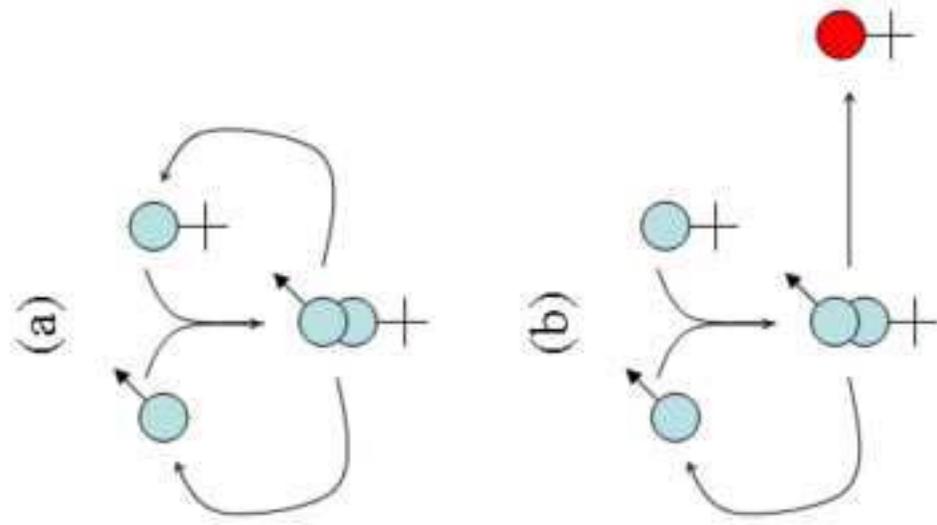
566

567

568

569

570



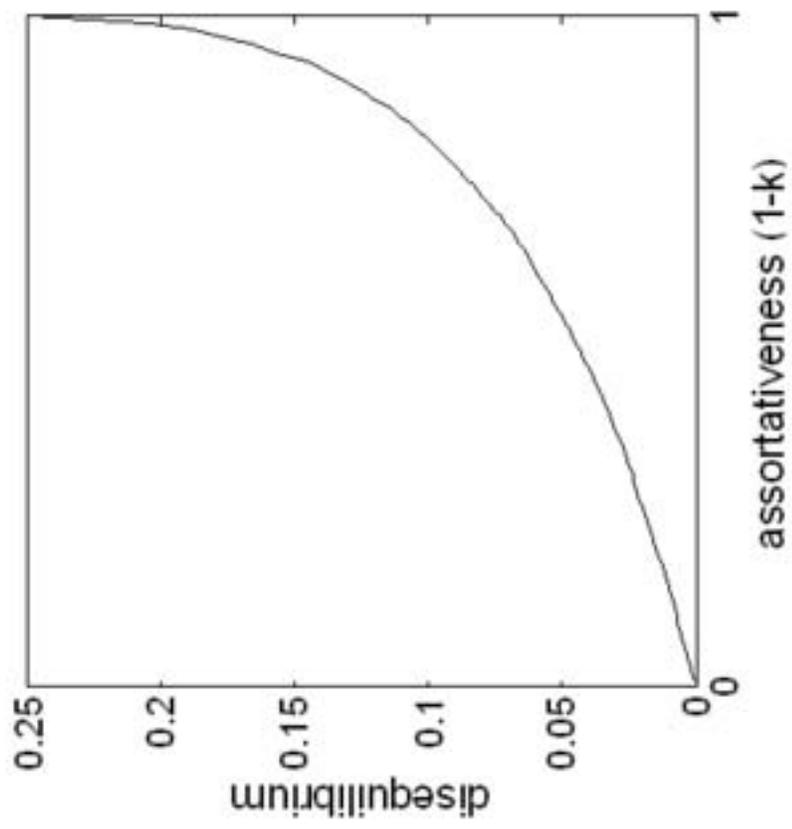
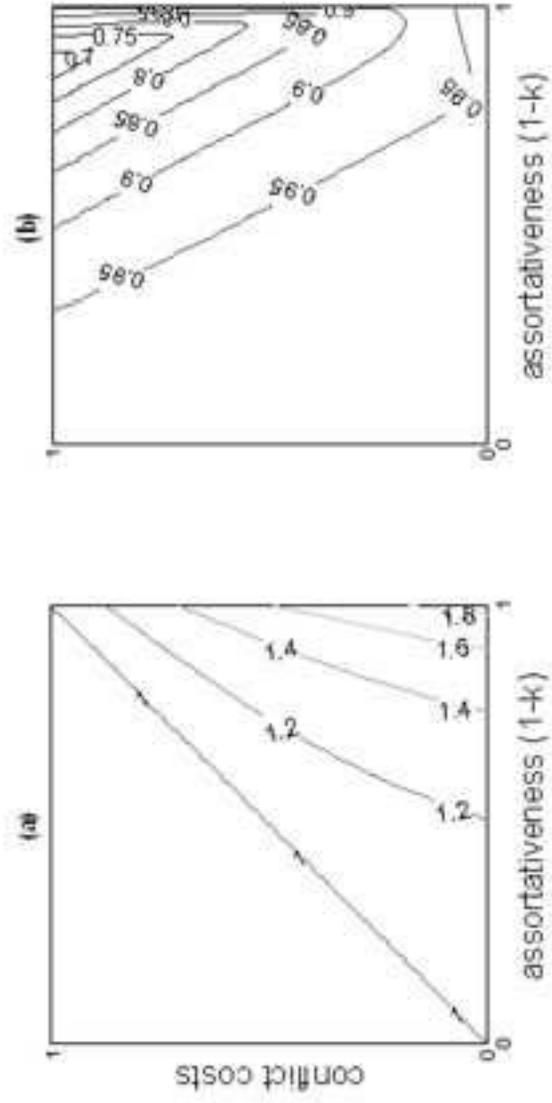


Figure 2



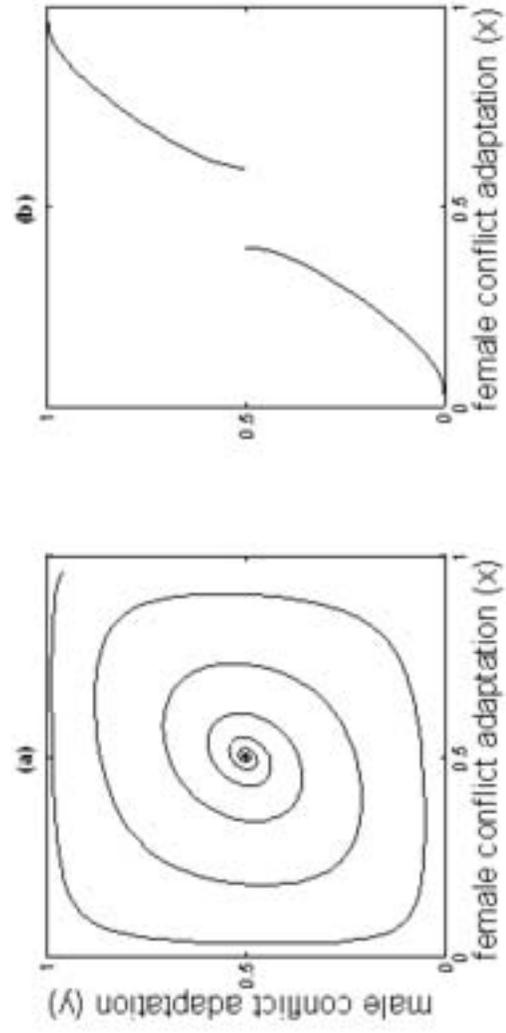


Table 1. Mating table for the type matching mating systems.

Mating type		Frequency	Fitness	Offspring			
Male	Female			x_1y_1	x_1y_2	x_2y_1	x_2y_2
z_1y_1	z_1y_1	Ax_1^2	W_a	1	0	0	0
z_1y_1	z_1y_2	kBx_1x_2	W_b	$\frac{1}{2}$	$\frac{1}{2}$	0	0
z_1y_1	z_2y_1	Ax_1x_3	W_a	$\frac{1}{2}$	0	$\frac{1}{2}$	0
z_1y_1	z_2y_2	kBx_1x_4	W_b	$\frac{1}{2}(1-r)$	$\frac{1}{2}r$	$\frac{1}{2}r$	$\frac{1}{2}(1-r)$
z_1y_2	z_1y_1	Ax_2x_1	W_a	$\frac{1}{2}$	$\frac{1}{2}$	0	0
z_1y_2	z_1y_2	kBx_2^2	W_b	0	1	0	0
z_1y_2	z_2y_1	Ax_2x_3	W_a	$\frac{1}{2}r$	$\frac{1}{2}(1-r)$	$\frac{1}{2}(1-r)$	$\frac{1}{2}r$
z_1y_2	z_2y_2	kBx_2x_4	W_b	0	$\frac{1}{2}$	0	$\frac{1}{2}$
z_2y_1	z_1y_1	kAx_3x_1	W_a	$\frac{1}{2}$	0	$\frac{1}{2}$	0
z_2y_1	z_1y_2	Bx_3x_2	W_b	$\frac{1}{2}r$	$\frac{1}{2}(1-r)$	$\frac{1}{2}(1-r)$	$\frac{1}{2}r$
z_2y_1	z_2y_1	kAx_3^2	W_a	0	0	1	0
z_2y_1	z_2y_2	Bx_3x_4	W_b	0	0	$\frac{1}{2}$	$\frac{1}{2}$
z_2y_2	z_1y_1	kAx_4x_1	W_a	$\frac{1}{2}(1-r)$	$\frac{1}{2}r$	$\frac{1}{2}r$	$\frac{1}{2}(1-r)$
z_2y_2	z_1y_2	Bx_4x_2	W_b	0	$\frac{1}{2}$	0	$\frac{1}{2}$
z_2y_2	z_2y_1	kAx_4x_3	W_a	0	0	$\frac{1}{2}$	$\frac{1}{2}$
z_2y_2	z_2y_2	Bx_4^2	W_b	0	0	0	1