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# Stable bifurcations in semelparous Leslie models<sup>†</sup>

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In this paper, we consider nonlinear Leslie models for the dynamics of semelparous age-structured populations. We establish stability and instability criteria for positive equilibria that bifurcate from the extinction equilibrium at  $R_0 = 1$ . When the bifurcation is to the right (forward or super-critical), the criteria consist of inequalities involving the (low-density) between-class and within-class competition intensities. Roughly speaking, stability (respectively, instability) occurs if between-class competition is weaker (respectively, stronger) than within-class competition. When the bifurcation is to the left (backward or sub-critical), the bifurcating equilibria are unstable. We also give criteria that determine whether the boundary of the positive cone is an attractor or a repeller. These general criteria contribute to the study of dynamic dichotomies, known to occur in lower dimensional semelparous Leslie models, between equilibration and age-cohort-synchronized oscillations.

Keywords: nonlinear age-structured population dynamics; Leslie matrix; semelparity; bifurcation; equilibrium; synchronous cycles; stability

# 1. Introduction

The inherent net reproductive number  $R_0$  is a basic quantity that can determine the viability of a biological population. The typical scenario is that a population at low density is threatened with extinction when  $R_0 < 1$  and can persist if  $R_0 > 1$ . Mathematically, an equilibrium in which the population is absent is (locally asymptotically) stable if  $R_0 < 1$  and is unstable if  $R_0 > 1$ . (Indeed, it is generally the case that uniform persistence or permanence, with respect to the extinction state, occurs when  $R_0 > 1$ .) The result of this destabilization as  $R_0$  increases through 1 is a transcritical bifurcation in which a branch of non-extinction equilibria intersects the extinction equilibrium at  $R_0 = 1$ . For  $R_0 = 1$ , this intersecting branch of non-trivial equilibria decomposes into two subbranches, corresponding to  $R_0 = 1$  and  $R_0 = 1$ , respectively, one of which consists of positive equilibria (the other consists of non-positive, and therefore biologically irrelevant, equilibria).

The general exchange of stability principle implies that stability is passed from the extinction equilibrium to the non-extinction equilibria as  $R_0$  increases through 1. We say that the bifurcating

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present at each point in time) always bifurcates from the extinction state at  $R_0 = 1$ , along with the positive equilibria [7]. This dynamic – periodic oscillations with non-overlapping age classes – is obviously quite different from that of the positive equilibrium – equilibration with all age classes present. Moreover, other cycles with two or more non-empty classes per time step can, under some circumstances, also bifurcate at  $R_0 = 1$  [8]. Although the dynamics on the boundary of the cone can be quite complicated, they nonetheless represent oscillations with missing age classes, which is in stark contrast to equilibration with all age classes present.

The number of age classes in the semelparous Leslie model (i.e. the dimension of the model) is essentially the length of the maturation period. For short maturation periods, that is, for semelparous Leslie models of dimension 2 or 3, it is known that a dynamic dichotomy exists between the bifurcation branch of positive equilibria and the boundary of the positive cone; namely, when Note that Equation (1) maps  $R_+$  into itself and  $R_+$  into itself.

We introduce the notation

$$_{j} = \begin{cases} 1 & \text{for } j = 1, \\ \prod_{j=1}^{j-1} & \text{for } j = 2, 3, \dots, \end{cases}$$
(3)

and define

$$R_0 \prod_{=1}$$
,

the inherent net reproductive number (i.e. the expected number of offspring per newborn per life time in the absence of density effects). We can introduce  $R_0$  explicitly into the model equations by writing

Using the notation

#### 3. Stability criteria for bifurcating positive equilibria

Our main result is in the following theorem, the proof of which is given in Appendix 1.

THEOREM 3 A e A1 a A2 h. We have the f i g bif cati e t f the e e a Le ie e (1) a (2) at  $R_0 = 1$ :

(a) I the ca e f a ight ( e -c itica) bif cati (i.e. he a<sub>1</sub> < 0), the bif cati g iti e e i ib ia i The e 2 a e, f R<sub>0</sub> 1, ( ca a t tica ) tabe if a a < 0 f = 2,3,..., 1/2 + 1. The a e tabe if a > 0 f at ea t e = 2,3,..., 1/2 + 1.
(b) I the ca e f a eft ( b-c itica) bif cati (i.e. he a<sub>1</sub> > 0), the bif cati g iti e e i ib ia i The e 2 a e, f R<sub>0</sub> 1, tab e.

For a left bifurcation to occur, sufficiently strong positive feedback or Allee effects are required (as represented by the derivatives  $_{j}^{0} > 0$  appearing in  $a_1$ ). We see from Theorem 3 that the bifurcating positive equilibria are always unstable in this case. In the case of a right bifurcation, however, the bifurcating positive equilibria might or might not be stable. That is to say, the direction of bifurcation does not always determine stability, as occurring in models with primitive projection matrices [6,9]. One case in which the direction of bifurcation does determine the stability is that when there is no between-class competition, since then we have  $a_{i} = a_{1}$  for all  $a_{i}$ .

COROLLARY 1 A*e* A1 *a* A2 h íhaí bet ee -ca c а etiti cc . If  $a_1 =$ < 0, the the ( e -c itica ) bif cati g iti ee i ib ia i The e 2 ae, f = 1  $R_0$  1, ( ca a t tica ) tab e. If  $a_1 > 0$ , the the (b-c itica) bif cati g iti e e *i i b i a i The* e 2 *a e*, *f*  $R_0$ 1, íab e.

A sufficient condition for the stability criteria a < 0 to hold in the case of a right (super-critical) bifurcation is that there be weak between-class (relative to within-class) competition intensity,

calculate subscripts mod and write

$$a = \sum_{j=1}^{0} + \sum_{j=1}^{-1} \sum_{j=1}^{-1} \sum_{j=1}^{0} \sum_{j=1}^{-1} e_{j} e_{j} e_{j}$$
 (6)

We find it convenient to define the quantities

$$\frac{\sum_{j=1}^{j=1} j j^{0} j^{j+1}}{\sum_{j=1}^{j=1} 0}, \qquad = 1, 2, \dots, -1$$

The denominator is a measure of within-class competition (at low population densities) as based on the derivatives <sup>0</sup>. The derivative  $_{j}^{0}$   $_{j+}$  in the numerator measures the effect that the density of the *j*th age class has on the survivorship of age class j + modulo. This means that the numerator in is a measure of the intensity of competition among these selected (but not all) unidirectional pairings of age classes. A little reflection shows that the competitive pairings among the remaining classes whose ages are units apart appear in the numerator of \_\_\_\_\_. As a result, the sum \_+ \_\_\_\_ measures the total effect of competition among all classes that are units apart (relative to within-class competition intensity).

We begin with two examples. First, we consider the case = 2 known as Ebenman's model [11, 18,19]. According to Theorem 3, the bifurcating positive equilibria are stable if

$$a_{2} = \sum_{=1}^{2} \quad ^{0} \quad + \sum_{j=1}^{2} _{j} _{j} _{j+1}^{0} (-1) < 0$$

or equivalently

The positive equilibria are unstable if this inequality is reversed. (This is the same result obtained in [7,11].) Thus, a stable (unstable) equilibrium bifurcation occurs when there is weak (strong) between-class competition in the sense that  $_{-1} < 1$  ( $_{-1} > 1$ ).

A similar result holds for the case = 3. According to Theorem 3, the bifurcating positive equilibria are stable if

$$a_2 = \sum_{=1}^{3} 2$$

In general, from Equation (6) and the 2 -periodicity of cosine, we have

$$a = \sum_{i=1}^{n} {}^{0} + \sum_{i=1}^{-1} \sum_{j=1}^{n} {}^{j}_{j} {}^{0}_{j+} \cos\left(\frac{2}{-1}(-1)\right)$$
$$= \sum_{i=1}^{n} {}^{0} + \sum_{i=1}^{-1} \cos\left(\frac{2}{-1}\right)$$

and the stability inequalities for even are

$$1 + B_{, 1/2} + \sum_{i=1}^{1/2^{-1}} B_{, i} ( + _{-}) > 0, = 2, \dots, _{1/2} + 1.$$
 (10)

Instability results if at least one inequality is reversed in Equations (9) and (10).

We can summarize these results with the following notation. For any matrix P = (j), define  $\cos(P) - (\cos(j))$ . Let *M* be the  $1/2 \times 1/2$  matrix whose entries are the products of the row and column indices, that is, M = (j). Note that, by the 2 -periodicity of cosine and by identity (8), we have

$$\cos\left(\frac{2}{-}M\right) = \left(\cos\left(\frac{2}{-}j\right)\right) = \left(\cos\left(\frac{2}{-}[j] \mod \right)\right) = (B_{+1,j}).$$

Define the 1/2-vectors

$$\hat{1} \quad \begin{pmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{pmatrix} \quad R_{+}^{1/2} \text{ and } \hat{} \quad \begin{pmatrix} 1 + & -1 \\ 2 + & -2 \\ \vdots \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & & \\$$

Rewriting Equations (9) and (10) and applying Theorem 3, we obtain the following result.

THEOREM 4 A e A1 a A3 h . The f  $R_0$  1, the bif cating it is e i ib ia i The e 3 a e ( ca a t tica ) tab e if

$$\hat{1} + \cos\left(\frac{2}{-M}\right) \hat{R}_{+}^{1/2}.$$
 (11)

The e i ib ia a e tab e if

$$\hat{1} + \cos\left(\frac{2}{-M}\right)^{-} / \bar{R}_{+}^{1/2}.$$
 (12)

The components + \_ of the vector  $\hat{}$  are measures of the total (relative) competition among age classes units apart. While there are -1 ratios , the stability and instability criteria in Theorem 4 involve only  $_{1/2}$  quantities. The  $_{1/2}$ 

Table 1. Criteria (11) for the stability of the bifurcating positive equilibria for  $R_0 \gtrsim 1$ .

	The stability criteria (11)
2	1 - 1 > 0
3	$1 - \frac{1}{2}(1 + 2) > 0$
4	$1 - \frac{2}{2} > 0$ 1 - (1 + 3) + 2 > 0
5	$1 + \frac{\overline{5}-1}{4}(1+4) - \frac{\overline{5}+1}{4}(2+3) > 0$ $1 - \frac{\overline{5}+1}{4}(1+4) + \frac{\overline{5}-1}{4}(2+3) > 0$
6	$1 - 3 + \frac{1}{2}(1 + 5) - \frac{1}{2}(2 + 4) > 0$ $1 + 3 - \frac{1}{2}(1 + 5) - \frac{1}{2}(2 + 4) > 0$ 1 - 3 - (1 + 5) + (2 + 4) > 0

Note: The equilibria are unstable if (at least) one inequality is reversed.

classes are identical for all age classes. Then,

 $_{1} = _{1}(_{1})$  and  $= _{2}(_{1})$  for  $= 2, 3, \dots,$ 

and the competition ratios are

$$= \frac{\frac{0}{1}}{\frac{2}{0}} \frac{2}{1}$$
 for all  $= 2, \dots, -1.$ 

In this case, the criteria for stable bifurcating positive equilibria are

$$1 + \frac{\frac{0}{1-2}}{\frac{1}{1-1}} \sum_{i=1}^{-1} \cos\left(\frac{2}{-i} \left[(-1)\right] \mod \right] > 0 \quad \text{for} = 2, 3, \dots, \quad \frac{1}{2} + 1.$$

From Equation (A4) in Appendix 2, we have

$$\sum_{i=1}^{-1} \cos\left(\frac{2}{i} \left[(-1)\right] \mod \right] + 1 = 0$$

for  $= 2, 3, \ldots, \frac{1}{2} + 1$  and the stability criteria reduce to

$$\frac{\frac{0}{1-2}}{\frac{0}{1-1}} < 1.$$

The reverse inequality implies instability.

E a e 2 The semelparous LPA model is the = 3 dimensional semelparous Leslie model (1) and (2) with

$$1(^{\circ}) = 1,$$
  
 $2(^{\circ}) = \exp(-23),$   
 $3(^{\circ}) = \exp(-31) - 33,$ 

and  $_2 = 1$ . The well-known LPA model is the basic model used in extensive experimental studies of nonlinear dynamics involving the species *T ib i* (flour beetles) [4,12]. The LPA model is

# 4. Synchronous cycles and the boundary of the positive cone

We see from Theorem 3 that the bifurcating positive equilibria of the semelparous Leslie map (1) and (2) assured by Theorem 2 can be either stable or unstable, even in the case of a right (supercritical) bifurcation. If the positive equilibria are unstable in the case of a right bifurcation, then for  $R_0$  1, both these and the extinction equilibria are unstable. In that case, a natural question to be asked is whether there is another bifurcating invariant set that is stable.

It was shown in [7] that, in addition to a branch of positive equilibria, there also bifurcates from the extinction equilibrium at  $R_0 = 1$  a branch of single-class -cycles. A single-class -cycle of Equations (1) and (2) is a periodic cycle of period in which exactly one class is present at each point in time:

$$\hat{}(1) = \begin{pmatrix} 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} \quad \hat{}(2) = \begin{pmatrix} 0 \\ 2 \\ (2) \\ \vdots \\ 0 \end{pmatrix} \quad \cdots \quad \hat{}(-) = \begin{pmatrix} 0 \\ 0 \\ \vdots \\ (-) \end{pmatrix} \quad \hat{}(1). \quad (14)$$

it follows that for every synchronous orbit we have

$$\lim_{t \to +} \frac{1}{t} \sum_{j=0}^{t-1} \ln \left( R_0 \prod_{j=1}^{t} (j), 2(j), \dots, (j) \right) = \frac{1}{t} \sum_{j=1}^{t} \ln \left( R_0 \prod_{j=1}^{t} (c(j)) \right),$$

where  $\hat{c}(t)$  approaches the cycle  $\hat{c}(t)$  of period . From [24, Theorem 4.1], we obtain the following result.

THEOREM 5 A e A3, A4 a A5 h . (a) The b a  $R_+$  f the iti e c e i a att act if  $\sum_{j=1} \ln \left( R_0 \prod_{i=1}^{n} (\hat{c}(j)) \right) < 0$ 

$$\sum_{j=1} \ln \left( R_0 \prod_{j=1}^{n} (\hat{c}(j)) \right) > 0$$

 $f e e ch e i ic c c e \hat{c}(j) R_+.$ 

Since there exists a single-class Reycle for

COROLLARY 3 A e A 3 a A 4

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For higher dimensional models, this dichotomy is an open question. Part of this question concerns the stability or instability of the bifurcating equilibria. The main result of this paper, Theorem 3, establishes stability and instability criteria for the bifurcating positive equilibria and 1 under general conditions and arbitrary dimension . Left (or sub-critical) bifurcations  $R_0$ always result in instability, as is expected. This occurs when positive feedback (Allee effects) in the dependence on survivorship and fecundity rates on population density occurs with sufficient strength. When negative density feedback predominates, the bifurcation is to the right (supercritical) and the criteria in Theorem 3 determine when the bifurcating equilibria are stable or unstable. While the number and details of these technical criteria, and hence their ecological interpretation, depend on the dimension of the Leslie model, one general conclusion that can be drawn is that stability occurs when between-class competition is weak relative to withinclass competition (Corollary 2). In the case when certain monotonicity conditions hold on the nonlinearities at least near the origin  $\hat{} = 0$ , we expressed in Theorem 4 the stability and instability criteria in terms of certain ratios that directly measure the relative competition intensity between age classes of fixed distances apart compared to within-class competition intensity.

The stability /instability criteria for bifurcating equilibria established in this paper address only part of the dynamic consequences that can result when a right (super-critical) bifurcation occurs at  $R_0 = 1$ . If the bifurcating equilibria are unstable, a question that arises (especially since the extinction equilibrium is also unstable) is what the attractor of orbits might be. Based on the known results for = 2 and 3, an attractor candidate in this case is the boundary of the positive cone (or synchronous cycles that lie on the boundary of the cone). In Section 4, we have given some criteria under which the boundary of the cone is in fact an attractor or a repeller. This question is not fully resolved for dimensions 4, however. While the dynamic dichotomy between the positive equilibria and the boundary of the positive cone has been established for models with specialized properties [10], the numerical example given in Section 4 suggests that perhaps the dichotomy does not hold in general.

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Let  $\hat{}$  () and  $\hat{}$  () denote the right and left eigenvectors of J() associated with ():

$$J()^{*}() = ()^{*}(),$$

$$(A3)$$

We denote the standard inner product of two vectors  $\hat{} = col()$  and  $\hat{} = row()$  by

$$\hat{}, \hat{} \doteq \sum_{i=1}^{n-1} \hat{}$$

,

where the bar in <sup>-</sup> denotes complex conjugation.

LEMMA A.1 F 0, e ha e the e a i

 $|()| = 1 + \operatorname{Re}((0)) - O(2).$ 

 $P \quad f \quad \text{Note} \mid (0) \mid = \mid = 1. \text{ Write } (0) = +i \text{ . Then,}$ 

$$|(i)|^{2} = \left| \cos\left(\frac{2(i-1)}{i}\right) + i\sin\left(\frac{2(i-1)}{i}\right) + (i+i) + O(2) \right|^{2}$$
$$= \left[ \cos\left(\frac{2(i-1)}{i}\right) + (i+i) + O(2) \right]^{2} + \left[ \sin\left(\frac{2(i-1)}{i}\right) + (i+i) + O(2) \right]^{2}$$

and

$$\frac{\mathrm{d}|(\ell)|}{\mathrm{d}|}\Big|_{=0} = \cos\left(\frac{2(\ell-1)}{\ell}\right) + \sin\left(\frac{2(\ell-1)}{\ell}\right).$$

From

$$\operatorname{Re}(-(0)) = \operatorname{Re}\left(\left[\cos\left(\frac{2(-1)}{-1}\right) - i\sin\left(\frac{2(-1)}{-1}\right)\right] \left[-i\right]\right)$$
$$= \cos\left(\frac{2(-1)}{-1}\right) + \sin\left(\frac{2(-1)}{-1}\right)$$

follows

LEMMA A.2 The ight a eff eige ect f J(0) a ciate ith eige a e a e

$$\mathbf{f}(\mathbf{0}) = \begin{pmatrix} 1 \\ 2 \\ -1 \\ 3 \\ -2 \\ 3 \\ \vdots \\ -(-1) \end{pmatrix}, \quad \mathbf{(0)} = \begin{pmatrix} -1 & -1 - & -1 - 2 \\ 1 & 2 \\ -1 & -1 - & -1 \end{pmatrix}.$$

Th , (0), (0) = .

P = f That these are eigenvectors is straightforwardly verified by substitution into the equations

$$J(0)^{(0)} = (0),$$
  
 $(0)J(0) = (0),$ 

and recalling definition (3) of .

The Jacobian evaluated at the equilibrium () and  $R_0 = 1 + has the additive form <math>J() = L() + M()$  where L() and M() are given by Equations (A1) and (A2). Therefore, from Lemma A.2, we have

This gives

$$L(0)^{-}(0) = \begin{pmatrix} \begin{pmatrix} -1 & -1a_{1}^{-1}\sum_{j=1}^{n} & j & 0 \\ -1a_{1}^{-1}\sum_{j=1}^{n} & j & j \end{pmatrix} \begin{pmatrix} -(-1) \\ -(-1a_{1}^{-1}\sum_{j=1}^{n} & j & j \end{pmatrix} \begin{pmatrix} -(-1) \\ -(-1a_{1}^{-1}\sum_{j=1}^{n} & j & j \end{pmatrix} \begin{pmatrix} -(-1) \\ -(-1a_{1}^{-1}\sum_{j=1}^{n} & j & j \end{pmatrix} \begin{pmatrix} -(-1) \\ -(-1a_{1}^{-1}\sum_{j=1}^{n} & j & j \end{pmatrix} \begin{pmatrix} -(-1) \\ -(-1a_{1}^{-1}\sum_{j=1}^{n} & j & j \end{pmatrix} \begin{pmatrix} -(-1) \\ -(-1a_{1}^{-1}\sum_{j=1}^{n} & j & j \end{pmatrix} \begin{pmatrix} -(-1) \\ -(-1a_{1}^{-1}\sum_{j=1}^{n} & j & j \end{pmatrix} \begin{pmatrix} -(-1) \\ -(-1a_{1}^{-1}\sum_{j=1}^{n} & j & j \end{pmatrix} \begin{pmatrix} -(-1) \\ -(-1a_{1}^{-1}\sum_{j=1}^{n} & j & j \end{pmatrix} \begin{pmatrix} -(-1) \\ -(-1) \end{pmatrix} \end{pmatrix}$$

Recalling definition (3) of , we have

$$L(0)^{-}(0) = \begin{pmatrix} \left(1 - a_{1}^{-1} \sum_{j=1}^{j} b_{j}^{0}\right) & 1 & -(-1) \\ \left(-a_{1}^{-1} \sum_{j=1}^{j} b_{j}^{0} & 1\right) & 2 \\ \left(-a_{1}^{-1} \sum_{j=1}^{j} b_{j}^{0} & 2\right) & 3 & -1 \\ & \vdots & & \\ \left(-a_{1}^{-1} \sum_{j=1}^{j} b_{j}^{0} & -1\right) & -(-2) \end{pmatrix}$$

and

$$(0), L(0)^{(-)}(0) = \prod_{1}^{-1} \left(1 - a_{1}^{-1} \sum_{j=1}^{-1} j - 1\right)^{-1}$$

100

LEMMA A.4 F (0) i Le a A.3, e ha e that

(0), 
$$M$$
 (0)  $(0) = -a_1^{-1} \sum_{j=1}^{\infty} \sum_{j=1}^{j} a_j^{-j}$ 

a he ce

$$(0) = -\frac{1}{a_1^{-1}} \sum_{i=1}^{n} \sum_{j=1}^{n} j_j j^{-1} - \frac{1}{a_1^{-1}}.$$

P = f From Equation (A2) evaluated at the equilibrium  $\hat{}$  ( ) and  $R_0 = 1 + \hat{}$ , we calculate

$$M(0) = \begin{pmatrix} -1 & 0 & (0) & -1 & 2 & 0 & (0) & \cdots & -1 & 0 & (0) \\ 1 & 1 & 1 & 1 & (0) & 1 & 2 & 1 & 1 & (0) & \cdots & 1 & 1 & 1 & 1 & (0) \\ \vdots & \vdots & \vdots & & \vdots & & \vdots & \vdots \\ -1 & 1 & -1 & -1 & (0) & -1 & 2 & 0 & -1 & -1 & (0) & \cdots & -1 & 0 & -1 & -1 & (0) \end{pmatrix},$$

from which we can calculate

$$M(0)^{-}(0) = \begin{pmatrix} -a_{1}^{-1} \sum_{j=1}^{j} j & 0 & -(j-1) \\ -2a_{1}^{-1} \sum_{j=1}^{j} j & j & 1 \\ -3a_{1}^{-1} \sum_{j=1}^{j} j & 2 & 0 & -(j-1) \\ \vdots & \vdots & \vdots \\ -a_{1}^{-1} \sum_{j=1}^{j} j & j & -1 & 0 \end{pmatrix}$$

and

$$(0), M \quad (0)^{\circ} \quad (0) = -a_1^{-1} \sum_{j=1}^{j} j^{0} \stackrel{-(j-1)}{-} - a_1^{-1} \sum_{j=1}^{j} j^{0} \stackrel{-(j-1)}{-} \\ - \frac{2a_1^{-1} \sum_{j=1}^{j} j^{0} \stackrel{-(j-1)}{-} - \cdots - \frac{-1a_1^{-1} \sum_{j=1}^{j} j^{0} \stackrel{-(j-1)}{-} }{-a_1^{-1} \sum_{j=1}^{j} j^{0} \stackrel{-(j-1)}{-} } \\ = -a_1^{-1} \sum_{j=1}^{j} j^{0} \stackrel{-(j-1)}{-} - a_1^{-1} \sum_{j=1}^{j} j^{0} \stackrel{-(j-1)}{-} \\ - a_1^{-1} \sum_{j=1}^{j} j^{0} \stackrel{2(0)}{-} - \cdots - a_1^{-1} \sum_{j=1}^{j} j^{0} \stackrel{-(j-1)}{-} ,$$

which yields the formula in the lemma.

# Appendix 2. A lemma

LEMMA A.6 F 2